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CONTRIBUTIONS FROM THE LABORATORY
OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

XXI

EXUVIATION, AUTOTOMY AND REGENERATION IN *CERATIUM*

BY
CHARLES ATWOOD KOFOID.

XXII

NOTES ON SOME OBSCURE SPECIES OF *CERATIUM*

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With the compliments of

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INTRODUCTION.

In view of Ostwald's (:03) able discussion of the physical factors of the pelagic environment and Nathanson's (:06) recent suggestive presentation of the phenomenon of vertical circulation in relation to the problems of plankton production, added interest attaches to all structural modifications and adaptations of the organisms constituting the plankton. New meaning and significance appear in characters which have long escaped notice or have been regarded as only additional instances of that wonderful variety of form and wide range of variation within the species which pelagic organisms are wont to exhibit.

In the present paper certain structural features in the skeletal parts of *Ceratium* giving evidence of changes of functional significance are described and these changes are correlated with the problem of flotation as modified by the vertical distribution of temperatures and the possibilities of vertical circulation of oceanic waters.

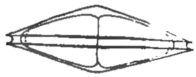
The genus *Ceratium* is noteworthy among pelagic unicellular organisms for the length and tenuity of the processes or horns which extend from the central midbody containing the nucleus and the main mass of the cytoplasm. In common with the rest of the body they are sheathed within a porulate cellulose wall or exoskeleton. These processes form the single apical and the two (in a few cases, three or more) antapical horns whose position, length, structure and angles of divergence exhibit a most remarkable variety in the scores of species known in the genus. These horns provide, as I have elsewhere (:08) shown, a functional adaptation to flotation and to orientation upon sinking, of prime importance to the species. In the course of my examination of the Dinoflagellates of the plankton of the Pacific off San Diego during the past seven years I have noted numerous instances of individuals with broken horns and many cases of regeneration, in the normal conditions attending the life of the various species in the pelagic habitat. It is the purpose of this paper to discuss these phenomena and the related one of exuviation in normal conditions of pelagic life, and inquire into their significance, es-

pecially with reference to the problem of flotation as affected by the extent and volume of the exoskelton.

The term "ecdysis" or "cytecdysis" will be applied to the process of shedding the entire cell wall at one time and usually in a single piece, in two pieces or in a more or less intact condition. The removal of the wall, plate by plate or in groups of plates of small extent may, on the other hand, be designated as exuviation or cytexuviation. In the first case the cell contents withdraw bodily from the theca, while in the other the cell wall is cast off in parts and with the resulting temporary combination of new and old skeletal parts on one individual.

Ecdysis.

1. *Occurrence in Dinoflagellata.*—In many Dinoflagellates the whole theca is abandoned by the daughter schizonts after schizogony and an entirely new exoskeleton is formed by each of the two or more daughter cells or swarm spores, as for example in *Pyrophacus horologicum* (figs. 1 and 2). At times in those genera in which the parental theca is shed at fission the cell contents may escape from the theca as a *Gymnodinium*-like, naked spore without preceding division, as in *Gonyaulax*, *Diplopsalis* (fig. 3), *Peridinium* (fig. 4) and *Glenodinium*. Subsequently, without intervening division, an entirely new theca is regenerated to replace that lost by this total and simultaneous ecdysis. The thecal plates are usually not dispersed but remain adherent to one another after the escape of the cell contents. Confinement in a crowded plankton collection under conditions of high temperature, more intense illumination than normal and considerable concentration of the products of plant and animal metabolism, induces spontaneously this total simultaneous ecdysis in many Dinoflagellates in the course of several hours after removal from the sea. It also appears to occur normally in the sea to a large extent in *Gonyaulax polyhedra* which forms the patches of "red water" off the coast of Southern California in late summer. In these swarms the numbers of *Gonyaulax* and other Dinoflagellates are so great that the concentration of the products of metabolism must approach that of an ordinary plankton collection, though



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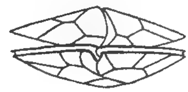

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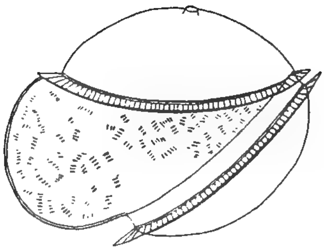

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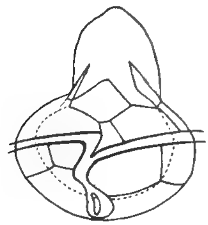

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Fig. 1.—Lateral view of *Pyrophacus horologicum* with swarm spores. × 300. After Schütt ('96).

Fig. 2.—Ventral view of the same after release of swarm spores by opening the girdle suture. × 300. After Schütt ('96).

Fig. 3.—*Diplopsalis lenticula* after treatment with alkali, showing contents escaping through the opened girdle suture. × 430. After Schütt ('95).

Fig. 4.—Ventral view of *Peridinium ovatum* showing spreading of the apical plates and the escape of the cell contents through the apical pore. × 240. After Schütt ('96).

the other environmental conditions such as temperature are not greatly modified. It seems probable that one or more of the changed relations in matters of metabolism brought about by these conditions may induce this total exuviation even in the normal habitat.

2. *Relation to schizogony.*—It is noteworthy that genera which most perfectly exhibit simultaneous ecdysis without attendant schizogony are, in the main, those which at fission and spore formation abandon entirely the parental theca. This is perhaps not a universal rule, for I have found in some species

of *Gonyaulax* unequivocal evidence of *typical oblique fission of the theca* in recent schizonts. In the genus *Ceratium* oblique fission of the theca or exoskeleton universally attends schizogony and the parental theca is shared by the daughter schizonts. Moreover in this genus no instance of *total* ecdysis has been noted in any of the numerous collections of living and preserved plankton which I have examined, neither from the crowded swarms in the "red water" or in condensed plankton collections which have stood in the laboratory for several hours. Fission of the theca in schizogony and entire absence of *total* simultaneous ecdysis thus appear to be the rule in the genus *Ceratium*. The possibility of the occurrence, however, of total ecdysis at the time of sexual reproduction must not be excluded.

Exuviation.

1. *Statement of the problem.*—It becomes, therefore, a matter of interest to consider the formation of the cell wall and the method by which the ancestral theca is passed on in asexual reproduction and what means, if any, exist for ridding the organism of the accumulating products of metabolism found in the cell wall, and of adapting these fixed skeletal structures to the changing environmental conditions which affect profoundly the capacity of the organism for flotation and maintenance in its position within the zone of optimum illumination in the upper levels of the sea.

2. *Structure of the cell wall.*—It is not my purpose to discuss the details of this subject which has been elaborately worked out by Schütt ('95, '99, and :00) but merely to call attention here to the facts pertinent to this discussion. The wall and its superficial modifications are formed of cellulose or of a substance closely allied to it, and the material is laid down on the periphery of the main mass of the cell plasma and its extensions in the apical and antapical horns. Its increase in thickness is brought about probably by appositional rather than intussceptional growth, centripetally on the inner, and centrifugally on the outer face of the wall, but principally by the latter process. Access to the outer face of the wall is gained through the many pores which are distributed in the wall in all regions, though more sparsely towards

the ends of the horns and less abundantly on the thin ventral plate (figs. 5 and 6). The plasma streams out through these pores (Schütt '99) in long filaments and may form an extramembranous sheet on the outer face of the exoskeleton. Both faces

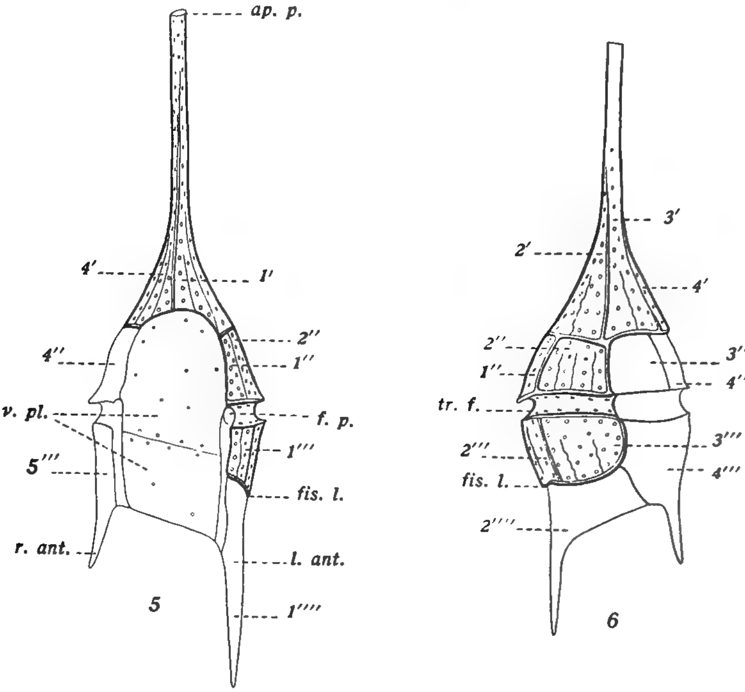

Fig. 5.—Ventral view of *Ceratium eugrammum*, an anterior schizont after recent division. × 913.

Fig. 6.—Dorsal view of the same. Regenerated moiety of the theca shown without pores. × 913.

Abbreviations—*ap. p.*, apical pore; *f. p.*, flagellar pore; *fis. l.*, fission line; *l. ant.*, left antapical; *r. ant.*, right antapical; *tr. f.*, transverse furrow; *v. pl.*, ventral plate; *1'-4'*, apical plates; *1''-4''*, precingular plates; *1'''-5'''*, postcingular plates; *1''''-2''''*, antapical plates.

of the cellulose wall are thus accessible to action of the cytoplasm in deposition or solution of the material of the wall.

The thickness of the wall and the extent of its surface differentiations in the form of lists, ribs, fins, and rugosities differ considerably in different species, ranging from the thin hyaline,

structureless, minutely porulate type seen in *C. trichoceros* (fig. 16) to the thick-walled, much ribbed and coarsely porulate one exemplified in *C. robustum* and *C. limulus.* In the normal course of asexual reproduction the type of wall characteristic of the species is maintained by immediate and rapid regeneration of

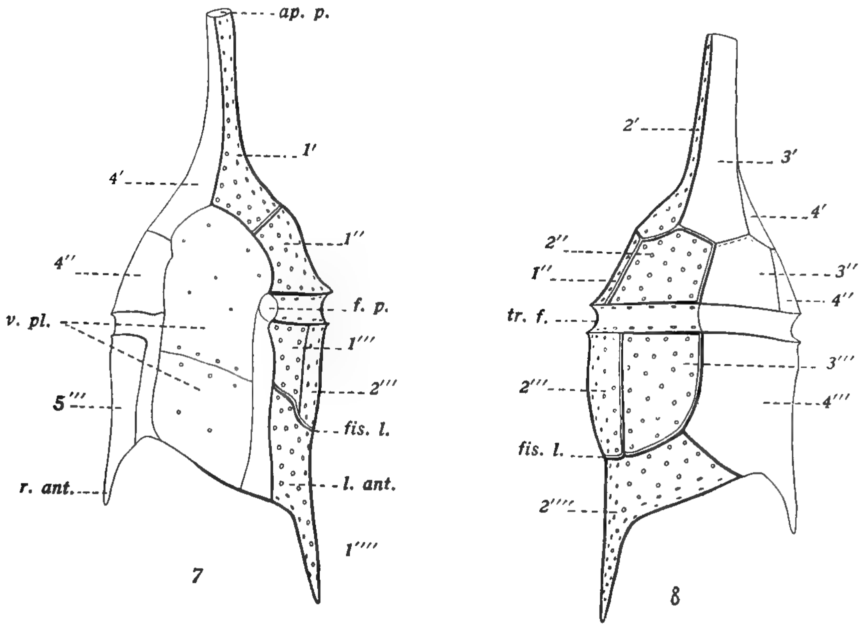

Fig. 7.—Ventral view of another individual after exuviation of part of the thecal plates. Senile theca with heavy sutures and pores. × 880.

Fig. 8.—Dorsal view of same. × 880.

(For explanation of abbreviations, see under figures 5 and 6.)

the new half of each skeleton at the time of schizogony. The differences between the newer and older thecal moieties of individuals recently divided and still in chain are usually obliterated by assimilative regeneration before the separation of the schizonts. On the other hand, within the limits of each species there is a rather wide range of wall structure between the more delicate and the more robust habits, which appears to be correlated with environmental conditions especially those affecting flotation. Occasionally heavily armored individuals of a species are found

whose habit is strongly suggestive of a senile condition and whose cell wall is apparently thickened by the accretions of long-continued growth. Obviously such structure must profoundly affect both metabolism and flotation, for it cuts down the access of light to the chromatophores of the cell on the one hand and on the other affects both specific gravity and specific surface.

3. *Transfer of the ancestral theca in schizogony.*—Asexual reproduction in *Ceratium* as in most Dinoflagellates and the flagellates generally, is accomplished by binary fission, though the

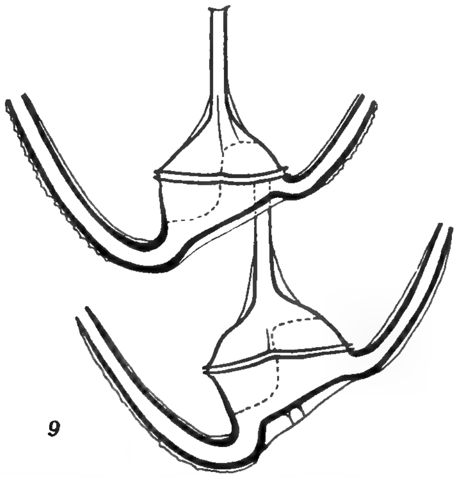

Fig. 9.—Dorsal view of *Ceratium vultur*, a form with short horns in chain showing compensatory character of newly formed thecal moieties, to wit, the two thecal halves between the dotted fission lines. The weight of the lines represents the relative thickness of the walls. × 220.

possibility of multiple spore formation can not be excluded. In the binary fission of *Ceratium*, as has been shown in detail by Lauterborn ('95) for *C. hirundinella*, and as may be seen in most recent schizonts (figs. 5 and 6), the plane of fission is not transverse but passes obliquely across the body from the right anterior to the left posterior margin, separating the parental theca into two parts. The anterior part includes the apical horn and precingular plates 1″ and 2″,[1] and postcingular plates 1′″, 2′″ and 3′″ with the left half of the girdle which is included between the two series of plates. On the dorsal face the suture

line crosses the girdle near the mid-dorsal line (fig. 6) but on the ventral face Lauterborn figures it as passing along the anterior margin of the ventral plate at the base of the apicals and down to the flagellar pore along the right margin of precingular 1′ ″ and thence through the longitudinal furrow along the right margin of postcingular 1′ ″ to the postcingular suture. Its course is outlined by a dotted line in figures 4 and 5. The posterior schizont receives the remainder of the plates, precingulars 3″ and 4″, postcingulars 4′ ″ and 5′ ″, antapicals 1″ ″ and 2″ ″ and the other half of the girdle plates as well as the ventral plate (Lauterborn '95). The right and left antapical horns thus belong to the posterior schizont, and the apical to the anterior one.

At the completion of each schizogony the parental theca is shared in this manner between the two schizonts, each of which regenerates during the process the missing half of the thecal exoskeleton. In chain formation (figs. 9 and 10) which ensues when schizogony is rapidly repeated the two parts of the ancestral theca are found respectively upon the anterior and posterior schizonts of the chain. It is evident that these ancestral portions may continue to form a part of the armor of some two of the offspring for an indefinite time unless some other type of reproduction intervenes, such as spore formation or conjugation, in which the cell contents abandon permanently the thecal exoskeleton of this vegetative period, or unless some modification of the usual physiological processes occurs by virtue of which the thecal wall is resolved or shed in whole or in part.

4. *Assimilative regeneration of the theca in schizogony.*—It might be supposed that these ancestral contributions could be detected readily by their senile characters, such as thickened wall, and excessive development of superficial ribs and lists and increased depth of color, but this does not appear to be the case. In many instances of chain formation which I have observed among various species of this genus I have yet to find an instance in which the older and newer portions of the thecae of the anterior and posterior schizonts of a chain showed any considerable difference in their structural characters suggestive of a senile

[1] I have elsewhere (:07) described the thecal plates of *Ceratium* and proposed the nomenclature here employed.

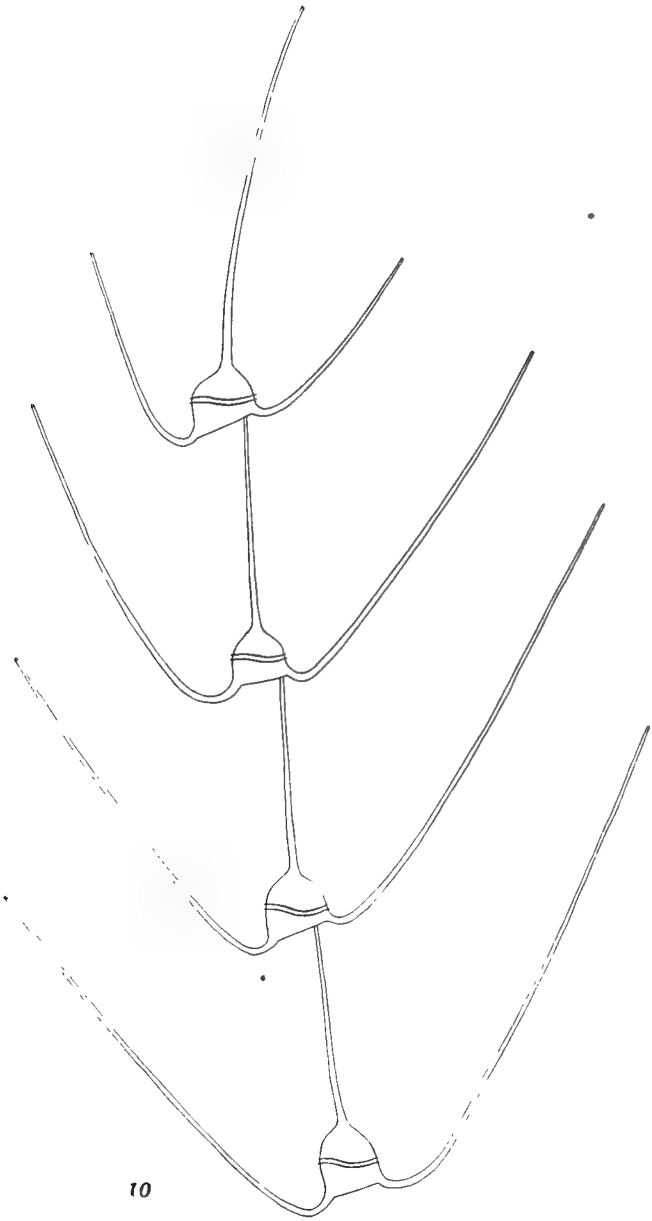

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Fig. 10.—Dorsal view of *Ceratium protuberans* (Karsten) in chain. × 100.

condition. This uniformity of skeletal facies is due to the compensatory or assimilative nature of the process of skeletal formation on the newer parts. As a rule a schizont with a rugged, robust, rugose and heavily ribbed ancestral moiety regenerates the lacking part of the thecal wall of a corresponding facies. It is true that schizonts in process of division, or very recently divided, will often have the ancestral portion of the theca upon one side of the fission line of a heavy facies, and upon the other side the recently formed part of more or less delicate habit. Such a condition is, however, temporary and quickly disappears, for it is apparent in the members of a chain of schizonts only in those rare instances where two adjacent individuals have been observed during or immediately after division. The remainder of the chain will be in almost all instances of uniformly rugged or delicate habit (fig. 10) according to the facies of the species or local environmental conditions. Evidence at hand indicates that in marine species chain formation takes place in the course of a few hours in the night. The rapidity of division and of regeneration of the lacking skeletal moiety and the compensatory nature of regeneration serve to obliterate to a large extent the distinctions between the skeletal parts of earlier and later formation. We have in this phenomenon a type of compensatory regulation which preserves in the new individuals the balance of skeletal parts and thus provides for normal locomotion and for orientation by gravity.

5. *Occurrence of senile forms in Ceratium.*—It seems quite probable that long periods of schizogony may prevail in the marine species of this genus. Sexual reproduction and spore formation are, as yet, wholly unknown in any marine forms. Zederbauer (:04 and :04*a*) has observed the former in *C. hirundinella*, a fresh water species, and spore formation among species in that habitat has long been known. If these types of reproduction occur, as they doubtless do, among the marine forms also, they are certainly elusive and possibly rare.

Given a long continued period of schizogony accompanied by some degree of assimilative regeneration of the newly formed portions of the theca in the cases of those schizonts which carry respectively the anterior and posterior moieties of the primal

ancestral theca, we find at once a basis for senility of skeletal parts in *Ceratium*. The origin of this primal theca is as yet unknown, though it may well be supposed to have been formed after an as yet undiscovered (for marine species) phase of sexual reproduction or spore formation in which all parts of prior ancestral thecae were abandoned. It seems probable, therefore, that heavily armored or senile individuals of the various species which are found in any extensive collection of marine plankton owe their origin to the slow accumulation of cellulose on the older thecal moiety and to the accompanying assimilative regeneration which gives a correspondingly rugose or senile aspect to the more recently formed part of the theca, and thus to the whole organism.

It is obvious that the senility here described refers strictly only to the formed skeletal part of ancestral origin and does not apply to the other half of the skeleton or to the cell body. It is therefore a pseudo-senility. Actual senility of the whole organism following upon a long-continued cessation of schizogony has not been detected by me, as such, though detached individuals of senile facies may, indeed, belong to that category.

6. *Removal of wall by solution.*—As before stated, total simultaneous ecdysis which would at once rid the organism of its impeding armor has not been observed in *Ceratium*. Two other possible methods of removal suggest themselves: partial exuviation and the resolution of the wall by the enveloping plasma. No evidence of the latter method has been noted beyond the fact of local solution in autotomy of the horns. Obviously it would be difficult to detect, except by observation during the process. Furthermore, it is probable that if it occurs it would exhibit the same regulatory correlation that is found in thecal formation and result in a reduction of all parts of the theca to a similar type or facies of wall and would, therefore, be difficult to detect.

7. *Evidence of exuviation in Ceratium.*—The removal of the thecal wall by exuviation or progressive shedding of thecal plates has not been hitherto reported. It is, however, easily overlooked and the process may well be more general than the data in hand indicate. Evidence of this method of removal of a greatly thickened ancestral wall, probably at the time of fission in this in-

stance, is to be found in figures 11 and 12. In a collection of plankton of semitropical contents taken off San Diego in July, 1905, there occurred a *Ceratium arcuatum* (?) which exhibited unequivocal evidence of recent exuviation. As will be seen in the figures the specimen is possibly the anterior schizont of a recent division. The posterior segment of the theca, separated from

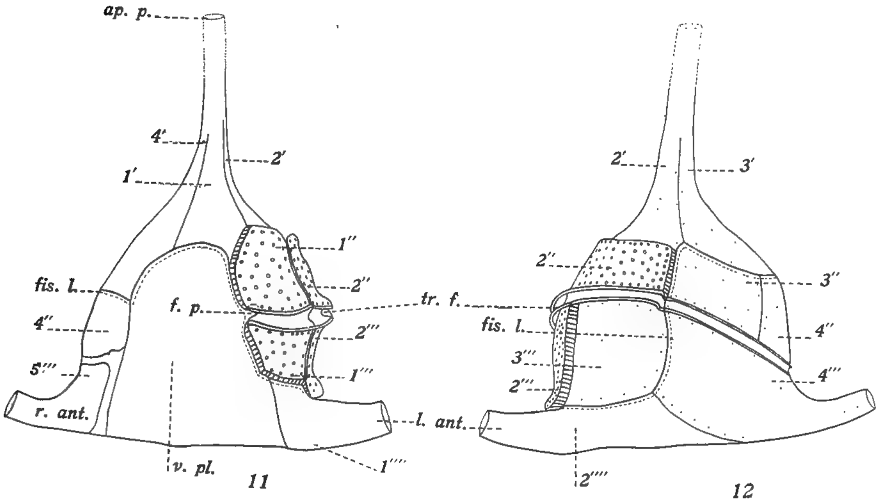

Fig. 11.—Ventral view of *Ceratium arcuatum* (?) in process of exuviation. × 375.

Fig. 12.—Dorsal view of the same. × 375. After sketches by Miss Marie Griffiths.

Specific identification is uncertain in the absence of the complete antapical horns. Precingulars *1''* and *2''* and post-cingulars *1' ''* and *2' ''* and adjacent girdle are senile plates. The others are all of recent formation.

the anterior by a dotted line in the figures, was very thin-walled and bore all the signs of recent formation. The anterior segment on the other hand had certain plates with strongly marked senile characters while its other plates were of very recent origin, being in fact visible only as exceedingly thin films. The senile plates, four in number, including precingulars 1'' and 2'' and postcingulars 1' '' and 2' '', together with those segments of the girdle plates which go to the anterior schizont in division, were exceedingly thick-walled, with a rugose surface deeply pitted by

well-developed pores. They did not merge gradually into the thin plates upon which they abutted but dropped off abruptly at the suture lines. Their thickness was not less than five times that of the adjacent new plates. The thin-walled plates of the anterior schizont included the four apicals, 1′-4′ and precingulars 3″ and 4″ They were uniformly thin and hyaline and their pores were scarcely visible. The plates of the apical series were least regenerated, and were, indeed, barely formed at the distal end of the apical horn.

The condition of all three horns in this specimen was indicative of their recent autotomy. In *C arcuatum* in normal condition (fig. 25) the antapicals are much longer than in this specimen and have pointed closed tips. The apical is also normally of at least twice the length in this individual. In this specimen all three horns are abnormally short and the antapicals are abruptly truncated and open. The three horns are, moreover, roughly still in the normal proportions of the horns in *arcuatum* to which species this individual appears to belong. The autotomy of the two antapicals is here attended by a proportionate reduction in the length of the apical.

The conditions here presented by this specimen unquestionably indicate a process of exuviation in which a thecal wall of senile character is in the process of being dropped off plate by plate and replaced by a new wall of delicate texture. The organism does not abandon its old theca as do *Glenodinium* and *Gonyaulax*, but drops it off piece-meal. Of the fifteen main plates of the theca but four here remain of the old type.

It may be significant in this specimen that all four of these plates belong to the *anterior* segment. It is thus possible that this exuviation attended schizogony and that the anterior segment shed its plates and regenerated new ones of a type similar to those forming on the posterior segment as a result of the formation after schizogony of new plates over the whole body, beneath the old on the anterior segment as well as over the posterior segment. The formation of the new plates beneath the old on the anterior moiety would result in the release and falling apart of the superimposed old plates of the anterior segment. It seems probable also that autotomy of the horns of a regulative or com-

pensatory character accompanied or preceded this process of exuviation in this individual.

Another instance of progressive exuviation which is not, however, accompanied by either autotomy or schizogony was noted in *C. eugrammum*, in a collection taken July 1, 1905, from the surface off San Diego. Dorsal and ventral views of this specimen are shown in figures 7 and 8. The right half of the theca is composed of delicate hyaline plates, in which the pores are scarcely visible. The left half, on the other hand, is made up of thick, deeply pitted plates. The line between the two contrasted areas is nearly longitudinal and does not follow the oblique fission line, as will be seen on comparison of the theca of this individual with one after normal fission shown in figures 5 and 6. The heavy portion of the exuviating individual contains most of the plates of the anterior moiety of a recent schizont. It lacks, however, apicals 1′ and 2′ and includes antapicals 1′′′′ and 2′′′′ which belong to the posterior moiety. The hyaline portion of this exuviating individual, which represents approximately the right half of the theca, includes apicals 1′ and 2′ which belong to the anterior moiety and lacks antapicals 1′′′′ and 2′′′′ It seems probable that the senile thecal wall in the right has been exuviated recently and replaced by the new hyaline wall. The distribution of senile plates in both moieties of the theca is conclusive evidence that normal schizogony has not occurred in conjunction with this instance of exuviation, but the possibility of an *abnormally* located fission plane is not necessarily excluded. No instance of abnormally located fission planes has been observed by me in any Dinoflagellate. A number of other instances of partial exuviation were noted in this same collection in *C. gallicum*, *C. inflexum*, and *C. carriense*, and have since been observed by me in these species in other collections.

8. *Significance of exuviation.*—It is obvious that the removal of the heavy senile wall makes possible a restoration of the normal conditions of illumination of the chromatophores and facilitates adjustment of the specific gravity and specific surface to the environmental factors governing flotation. In the collection of plankton in which this exuviating individual was found there was an unusual number of instances of autotomy of the horns in

the various species of *Ceratium* represented. The collection had a semi-tropical facies, including such species as *C. trichoceros*, *C. gallicum* and *C. biceps*. We find in this exuviation an apparent adaptation to changed conditions of flotation. This plankton of semi-tropical aspect may be brought to the San Diego region by occasional invasions of water from the south, possibly by northward extensions of the in-shore counter current which has been reported off Lower California.[2] There is also the possibility that plankton of the warmer surface waters may at times, if not constantly, sink to lower and colder levels. Organisms of the plankton drifting northward or sinking to lower levels are thus brought into regions of lower temperature with increased molecular friction which makes possible a reduction in specific surface. Such a reduction is brought about by the exuviation of the old theca with its lists and rugose surface and its replacement by the smoother new wall, and also by the dropping off of the outer ends of the antapical horns or of all three horns.

NORMAL AUTOTOMY IN CERATIUM.

Any observer of marine plankton will have his attention often called to the large number of individuals of *Ceratium*, especially of the longer-horned forms such as *C. biceps*, and many species of the *C. tripos* and *C. macroceros* groups, in which the horns appear to have been broken off. These mutilations are in some cases plainly of the nature of accidental breakages such as might come to pass in the exigencies of life in surface waters or result from collisions and rough handling which these delicate organisms undergo in the course of collection in the plankton net and in subsequent treatment of the material. The frequency with which mutilated individuals were found and especially their abundance in certain collections led me to suspect that other agencies than mere accident were at work in causing this phenomena in most of the mutilated individuals. A careful examination of accumulated data on this point indicates that autotomy of the horns is a normal phenomenon in *Ceratium*. The reasons for this conclusion are as follows:

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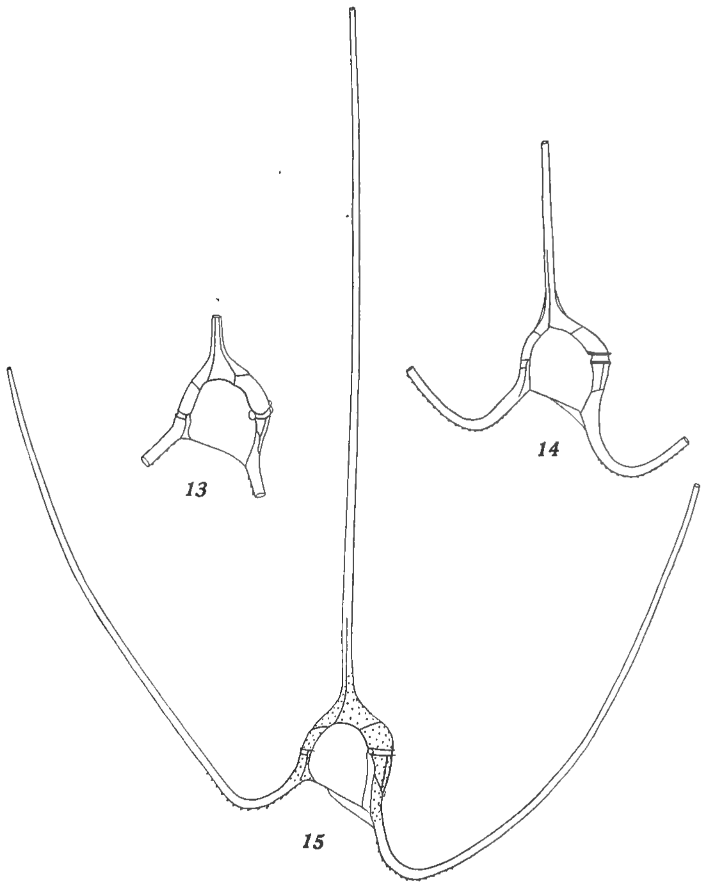
[2] See Quarterly Current Charts of the Hydrographic Department, British Admiralty ('97).

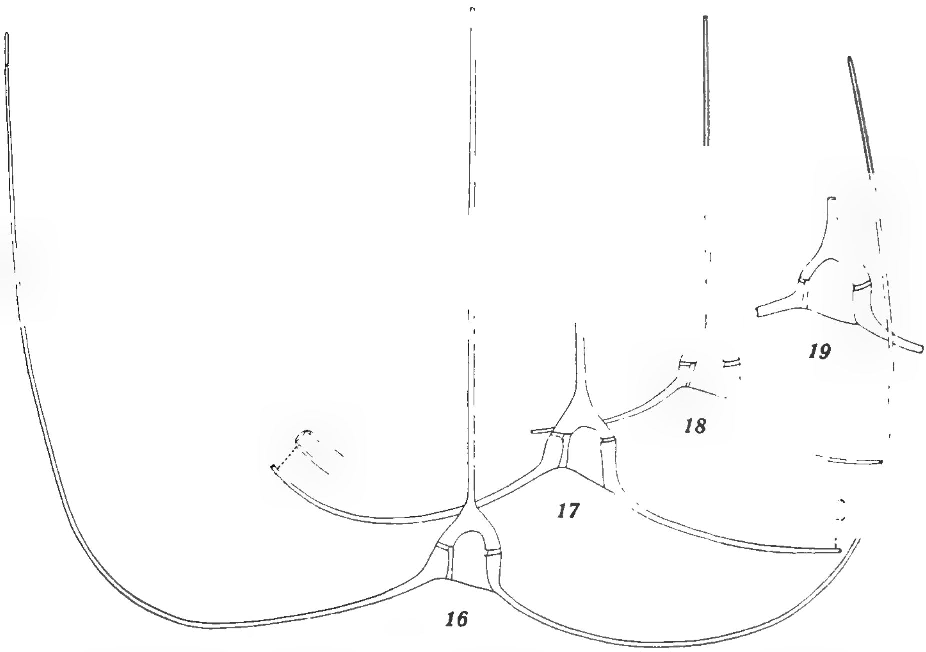
1. *Its general occurrence.*—Few collections from oceanic waters off San Diego in which *Ceratium* is found fail to contain some instances of autotomy. It appears, moreover, in practically all of the long-horned species belonging to the *C. tripos* and *C. macroceros* groups as well as in the more aberrant forms such as *C.*



Figs. 13-15.—Ventral views of *Ceratium gallicum* showing proportionate reduction of the horns in autotomy. × 220.

reticulatum and *C. clavipes.* The examination of a considerable range of collections at San Diego has afforded me evidence that this mutilation is more common in certain species, notably in *C. biceps, C. gallicum* (figs. 13-15) and *C. trichoceros* (figs. 16-19),

and appears occasionally in most of the species having elongated slender horns. I have observed it, for example, in *C. longipes*, *C. intermedium*, *C. protuberans* (fig. 20), *C. macroceros*, *C. ostenfeldi*, *C. vultur*, *C. inflexum*, *C. carriense*, *C. tripos*, *C. arcuatum* (figs. 11, 12, 26), *C. schranki*, *C. azoricum* and *C. hetero-*



Figs. 16-19.—Ventral views of *Ceratium trichoceros* showing progressive and proportionate reduction of the antapical horns in autotomy. × 220. The form of the end of the horns after autotomy is shown under greater magnification in supplementary sketches in connection with figure 17.

camptum. It occurs also in the long-horned members of the subgenus *Amphiceratium* such as *C. extensum* and *C. biceps* (figs. 21-24). It is, however, relatively rare among the species of the subgenus *Biceratium* such as *C. furca*, *C. lineatum* and *C. eugrammum*, where the antapical horns, and the apical also as a rule, are relatively short and play a less important part in the economy of flotation than they do in the long-horned species of the subgenera *Euceratium* and *Amphiceratium*.

2. *It is more frequently found in collections from deep water* (50-100 fathoms) than in those from the surface. It is also more abundant in collections of tropical facies occurring at San Diego than it is in those made up of species of more northerly distribution. Not infrequently, especially in the winter of 1904, the plankton collections taken off San Diego were unusually rich in species characteristic of the warmer seas, and at such times the proportion of mutilated *Ceratium* was unusually large.

Instances of autotomy of the horns of *Ceratium* occur also in surface collections made off San Diego. There is no evidence at hand to show whether these cases originate in these levels or are brought to the surface by the upwelling of colder water from lower levels a phenomenon known to occur along the California coast (see Holway '06) or by the aspiration of water from lower

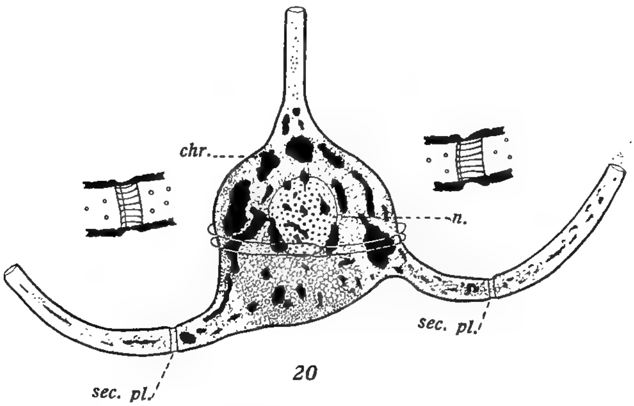


Fig. 20.—Dorsal view (somewhat oblique) of *Ceratium protuberans* in the process of autotomy. × 360. Supplementary sketches indicate the form of the section planes.

Abbreviations—*chr.*, chromatophores; *n.*, nucleus; *sec. pl.*, section plane.

levels in vortices formed between currents of tidal or oceanic nature flowing in opposite directions, as shown by Nathanson ('06).

3. *Evidence of autotomy.—(a) Formation of section planes.* The horns are cut off by the circular clefts, often though not always quite regular in form and transverse to the axis, which encircle the horns and form (fig. 20) wide V-shaped troughs, wider

at the surface, and steeper on the proximal face, which sink into the substance of the wall and sever it upon all sides. The superficial location of the troughs suggests the agency of the extramembranous plasma in bringing about a local resolution of the cellulose wall. I have found no indications of local solution on the inner face of the wall below the groove. There is no evidence of a withdrawal of the distal plasma from the outer part of the horn to the region proximal to the plane of section in individuals exhibiting the early phases of autotomy. Isolated horns found in the plankton with the proximal stump conforming to the section plane formed by autotomy, often contain a normal plasma core. The line of breakage formed by fracture is, on the other hand, usually an irregular ragged line often oblique to the axis of the horn.

(*b*) *Regulatory character of autotomy.*—One cannot fail to be impressed with the fact that a large proportion of the individuals exhibiting mutilation of the horns have either (1) both antapicals, or (2) all three horns cut off. This appears far in excess of the proportion demanded by the chances of accidental breakage. For example in a collection taken eleven miles off Point Loma on January 12, 1905, from a depth of 60 fathoms, a large number of individuals exhibit mutilation and of the first thirty-five observed in searching material with a mechanical stage no less than twenty-nine had both antapicals cut off, and twenty-six of these also had the apical similarly foreshortened.

The occurrence of individuals in which one or two horns have undergone autotomy while the other two or the third are still in the process is not unusual. An instance of this sort is shown in figure 24 of *C. biceps*, in which the apical is short, possibly as a result of recent autotomy, and the left antapical is nearly severed by two separate and distinct but adjacent section planes at a distance posterior to the girdle approximately proportional to the foreshortened apical horn. Such cases are suggestive of an approximation in the time of the autotomy of the two main horns of this species.

With a view of determining the extent and character of the processes of autotomy and of regeneration in a typical collection from deep water I made an examination of the plankton taken

with a No. 20 silk net, which presumably retains most of the small and short-horned forms of *Ceratium,* from a depth of ninety-six fathoms off San Diego, June 29, 1905. This catch was made by towing at this depth from a drifting boat for about 20 minutes. The net is in action, however, during both the descent to and ascent from this depth. The net presumably obtained a large proportion of its catch from lower levels but also filtered some water from the intervening and surface levels.

Samples withdrawn from the collection were examined with the aid of a mechanical stage and *all individuals of all species of Ceratium* were recorded with reference to their approach to the norm of the species as observed generally in oceanic plankton off San Diego. The length of the horns was measured in trans-diameters of the midbody at the girdle of the individual under observation, and the extent of regeneration, if present, was recorded for each of the horns in the same units. By this method the proportionate, compensatory, assimilative or regulatory character of the two processes of autotomy and regeneration of the horns is expressed quantitatively. Since every individual was recorded all elements of personal selection are eliminated.

The results are very striking in that they exhibit the extent to which autotomy and regeneration occurred within the limits between a depth of ninety-six fathoms and the surface and also the degree to which the processes of autotomy and regeneration are regulatory.

The first 125 individuals of Ceratium were recorded as shown in the accompanying table.

SPECIES OF CERATIUM.

	Normal	Showing autotomy	Showing regeneration	Regeneration without autotomy	Total examined
arcuatum	0	5	0	0	5
axiale	0	1	0	0	1
azoricum	0	4	1	0	4
biceps	8	16	1	1	26
bucephalum	1	0	0	0	1
candelabrum	3	0	0	0	3
carriense	0	2	0	0	2
deflexum	0	1	0	1	2
gallicum	1	6	3	0	7
heterocamptum	2	0	0	0	2
inflexum	1	13	7	2	16
intermedium	1	12	1	0	14
lineatum	5	1	1	0	7
longipes	4	10	3	2	16
macroceros	1	0	0	0	1
protuberans	0	8	0	0	8
seta	1	0	0	0	1
tenuissimum	1	1	1	0	1
teres	1	0	1	0	1
tripos	1	5	0	0	6
vultur	1	0	0	0	1
Total	32	85	19	6	125

These belonged to 21 species, of which 15 were represented in part or wholly by normal individuals, that is by those in which neither autotomy nor regeneration, either with or without preceding autotomy, was evident. In species of the *C. tripos* group autotomy is revealed by the opened tips. In species of the *C. macroceros* group, *carriense*, *deflexum*, *intermedium*, *longipes*, *protuberans*, *tenuissimum* and *vultur*, which normally have open tips, autotomy is only made evident when the arms are appreciably shortened by the process. The detection of individuals in which autotomy had occurred in these species is therefore a matter of judgment and liable to error or prejudice especially in cases approaching the norm of the species. My judgment as to the norm is based upon my impressions after some years of experience in examination of these species and upon the records of many measurements and comparisons with many camera drawings.

But 5 of the 21 species, to wit: *candelabrum, heterocamptum, macroceros, seta* and *vultur* were represented *only* by normal individuals. This is of little significance except in the cases of *C. bucephalum, C. candelabrum, C. heterocamptum* and *C. seta* in which, according to my observations elsewhere, autotomy is relatively rare. It occurs very generally in *C. macroceros* and *C. vultur.* The *total number* of normal individuals was only 32 of the 125 or but 26%, all others showing either autotomy or regeneration or both.

Of the 21 species, 14 or 67% showed autotomy. Those in which it was not recorded being *C. bucephalum, C. candelabrum, C. heterocamptum, C. macroceros, C. seta, C. teres,* and *C. vultur.* It has been seen by me, however, elsewhere in all these species, but is more frequent in those with open tips, *C. macroceros* and *C. vultur.*

Of the 125 individuals 85 or 67% had undergone autotomy, and it was more abundant, moreover, in those species of most frequent occurrence. In the species represented by 4 or more individuals, *C. arcuatum, C. biceps, C. gallicum, C. inflexum, C. intermedium, C. lineatum, C. longipes, C. protuberans,* and *C. tripos,* were included 102 of the 125 individuals. The number of these in which autotomy had occurred was 79, or 77.4%. It is particularly frequent in *C. intermedium* and *C. inflexum.*

Regeneration on the other hand was much less frequent, appearing, after autotomy, in only 19 cases or 15% and without evidence of prior autotomy in but 6 cases or 5%. It is, perhaps, significant that 17 of the 25 instances of regeneration occur in three species *C. gallicum, C. inflexum,* and *C. longipes,* in all of which autotomy is very frequent.

To test the matter of the proportionality of the horns of individuals in which autotomy and regeneration or both have occurred I have taken the first fifty individuals found by the aid of the mechanical stage representing the following species, *C. gallicum, C. inflexum, C. intermedium, C. longipes, C. carriense, C. arcuatum,* and *C. biceps,* merely omitting all normal ones after the first. Measurements of the total lengths of the horns and of their regenerated portions, if any, are given in transdiameters at the girdle in the following table.

Species	Length of horns in transdiameters				Length of regenerated horns in transdiameters		
	Apical	Right	Left	Ratio	Apical	Right	Left
C. gallicum[2]	4.8	3.8	4.5	1.2	0	0	0
C. gallicum	3.1	1.1	1.7	1.5	0	0	0
C. gallicum	5.4	4.1	5.3	1.3	1.	0.7	0.6
C. gallicum	1.2	1.	1.1	1.1	0	0	0
C. gallicum[1]	7.2	4.5	5.	1.1	0	0	0
C. gallicum	4.6	3.	3.5	1.2	1.	0.6	0.3
C. gallicum	1.2	2.	1.7	0.85	0	0	0
C. gallicum	2.	0.7	1.2	1.7	0	0	0
C. gallicum	1.4	3.7	4.6	1.8	1.2	1.6	1.7
C. inflexum[2]	7.3	6.7	7.9	1.2	0	0.8	0.9
C. inflexum	4.1	3.5	3.3	1.	0.9	1.1	1.2
C. inflexum	5.2	4.6	5.4	1.2	0.7	1.1	1.1
C. inflexum	0.5	1.7	2.2	1.3	0	0	0
C. inflexum[3]	0.9	5.2	6.5	1.2	0	0.3	0.3
C. inflexum[3]	2.9	1.3	4.6	2.5	0	0	0
C. inflexum	4.	3.2	4.3	1.3	0	0.1	0.2
C. inflexum	4.3	3.7	3.8	1.03	0.9	0.9	1.1
C. inflexum	3.8	3.7	3.4	0.9	0	0	0
C. inflexum[3]	0.6	5.7	6.7	1.2	0.6	0.8	1.
C. inflexum	2.6	4.8	4.8	1.	0	1.2	1.
C. inflexum[3]	4.	1.3	3.7[5] 1.7	2.8 1.3			
C. intermedium[2]	3.8	3.2	3.6	1.1	0	0	0
C. intermedium	3.2	2.6	3.3	1.3	0	0.8	0.8
C. intermedium	2.2	2.3	2.4	1.	0	0	0
C. intermedium	1.5	0.5	0.6	1.2	0	0	0
C. intermedium[3]	0.8	1.3	2.4	1.8	0	0	0
C. intermedium	0.5	0.5	0.7	1.2	0	0	0
C. intermedium[3]	5.4	3.8	6.3	1.7	0	0	0
C. intermedium[3]	1.5	0.8	1.4	1.7	0	0	0
C. intermedium	2.3	4.[4] 2.8	3.7	0.9 1.3	0	0	0
C. intermedium[3]	1.8	5.	1.6	0.3	0	0	0
C. intermedium	2.2	1.8	2.3	1.3	0	0	0
C. intermedium	1.	1.5	1.5	1.	0	0	0
C. intermedium	1.	1.1	1.2	1.1	0	0	0
C. longipes[1]	3.	3.	3.	1.	0	0	0
C. longipes[2]	4.5	3.8	4.1	1.1	0.5	0.2	0.3
C. longipes	3.5	1.9	2.8	1.4	0	0	0
C. longipes ([1] ?)	4.	2.5	3.	1.2	0	0	0
C. longipes	0.4	0.3	0.3	1.0	0	0	0
C. longipes	1.2	0.6	0.8	1.3	0	0	0
C. longipes	0.4	0.7	0.8	1.1	0	0	0
C. longipes	1.1	0.6	0.7	1.1	0	0	0
C. longipes	2.	1.4	1.6	1.1	0	0	0
C. longipes[2]	5.5	4.7	5.2	1.1	0.6	0.8	1.1
C. carriense	1.6	1.4	1.7	1.2	0	0	0
C. arcuatum	0.7	0.6	0.8	1.3	0	0	0
C. biceps[1]	23.	0.7	30.	43.	0	0	0
C. biceps	14.1	0.8	11.1	14.	0	0	0
C. biceps	19.	0.8	10.5	13.	0	0	0
C. biceps	4.5	0.5	4.5	9.	0	0	0
C. biceps	3.	0.5	2.5	5.	0	0	0

[1] Normal. [2] Regeneration without indication of autotomy. [3] Autotomy not regulatory. [4] Two section planes at about 2.8. [5] Three section planes at about 1.7.

An examination of the details of this table brings out certain significant tendencies. These appear perhaps most clearly in *C. gallicum.* A presumably normal individual has the apical, right and left antapicals in the ratios of 4.8—3.8—4.5, in a second case 7.2—4.5—5.0. In the six cases of autotomy recorded the apical retains an excess in length in all but two instances and in both of these there was evidence of recent schizogony and active growth of the newly formed apical. It is also noticeable that in four cases a considerable shortening of the apical is attended by much foreshortened antapicals. In the two normal individuals included in the table the relative lengths of the right and left antapical are 1 to 1.2 and 1 to 1.1 respectively. The average for all records of this species in the tables is 1 to 1.25 and for the six which have undergone autotomy 1 to 1.27 (range .85 to 1.7). In all but one instance after autotomy or regeneration or both, the individuals of *C. gallicum* recorded in this table show the left horn slightly longer than the right. These processes are thus regulatory and tend to preserve the norm of the species.

An examination of the data of *C. inflexum* yields somewhat similar conclusions. There are three instances (5, 6 and 10 of the list) in which the apical is noticeably disproportionate. One at least of these (10) is due to recent schizogony. In the other nine cases there is a tendency for a short apical to accompany short antapicals. In all but two instances (2 and 9) the left horn exceeds or equals the right in length, as in *C. gallicum,* and in about the same ratios, averaging 1.26 (or omitting the aberrant 6 the average becomes 1.15). The normal relation of longer left and shorter right horn thus prevails in all but two cases of the twelve. One of the two instances (12) of disproportionately long right horn presents significantly no less than three incipient section planes forming in the longer right horn at about 1.7 transdiameters from the midbody. The completion of this incipient autotomy would bring the ratio of the antapicals to 1.3, nearly the norm for the species. The other case (6) of disproportionate length of antapicals shows not the least trace of approaching regulatory autotomy. In both of these the deficiency of the left horn is slight. The ratio of the two horns after autotomy is in general thus approximately the same as that

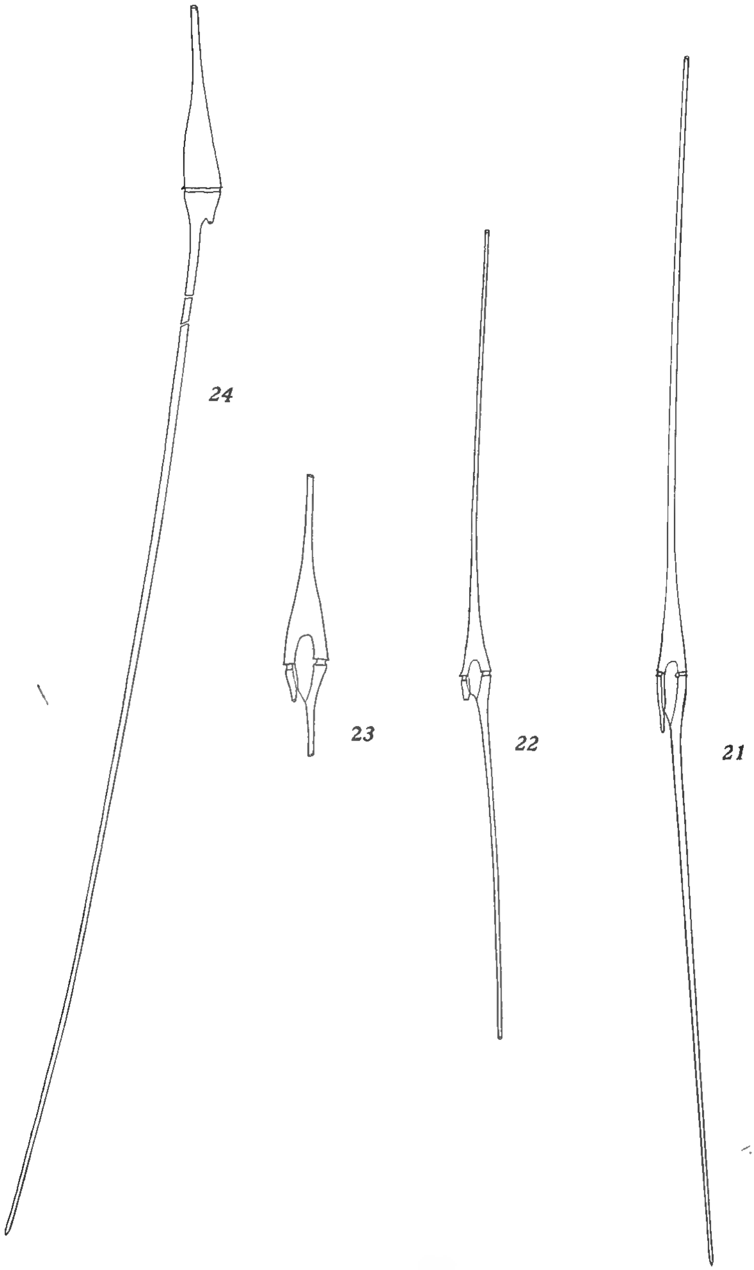
before the process. The first individual listed presents approximately normal conditions and has an antapical ratio of 1.2. With two exceptions in the table the ratios after autotomy lie between 1 and 1.3 or including the two cases of short left horns, between 0.9 and 1.3. The two exceptions both have disproportionately long left horns, that is the right horn has undergone autotomy while the left retains its primitive length.

In the main the data from *C. inflexum* support the view that both autotomy and regeneration are regulatory in this species. The exceptions are such as might attend schizogony or slight departures from coincident autotomy of the horns.

The data from *C. intermedium* are of similar import though somewhat more aberrant. In the thirteen instances there are five (5, 7, 8, 9 and 10) marked cases of disproportionate horns, that is of non-regulatory or possibly partially completed autotomy. One of these (9) has already two section planes at 2.8 transdiameters which when completed would bring the antapical ratio to 1.3, approximately the norm of the species. The remaining eight cases present antapical ratios, after autotomy ranging from 1 to 1.3.

In ten individuals of *C. longipes* there occurred seven instances of autotomy, all of which leave antapical ratios which fall within the limits 1.0 and 1.4, and five of them within 1.0 and 1.2. Similar regulatory relations in autotomy of the antapicals exist in the single individuals of *C. carriense* and *C. arcuatum* which are recorded in the table.

In *C. biceps* the right horn is always relatively very small and plays but little part in the mass relations and form resistance which control orientation and locomotion. Its autotomy and regeneration are, however, of frequent occurrence but are, it seems, often independent of these processes in the other horns. Autotomy of this horn is very frequent, much more so than that of the other horns. In many collections most of the individuals of this species will have the right horn truncated, as though there had been autotomy and subsequent healing without regenerative extension to the slender tapering antapex of typical form. Normal regeneration is, however, occasionally seen. As in other species so also in *C. biceps* there is a correlation in the autotomy



Figs. 21-23.—Ventral views of *Ceratium biceps* showing progressive and proportionate reduction in the apical and left antapical by autotomy. × 100.

Fig. 24.—Ventral view of *Ceratium biceps* after autotomy of the apical horn, showing two section planes, one of which is oblique, forming near the base of the left antapical. × 100.

of the horns. It is most apparent in the tendency toward a proportionate reduction of the large apical at the same time with the left antapical in autotomy. A very short apical is usually accompanied by a very short left antapical. The ratios of the antapicals of *C. biceps*, owing to their normal disproportion, are subject to extreme variations (figs. 21-24) in comparison with those in species having two large antapicals, as shown in the table.

The process of autotomy is thus of normal occurrence to a considerable extent in deep waters in a large number of species of *Ceratium* and is regulatory in character in the main.

Not only is autotomy found concidently, as a rule, in both antapicals, but it usually preserves approximately their relative lengths. As I have elsewhere shown (:07) the right antapical is formed by plates 4′″ and 5′″ of the postcingular series, while the left is formed entirely by the two plates of the more distal antapical series. This fact lies at the basis of the general occurrence in many of the species of *Ceratium* of an inequality in the length of the antapicals. The right is usually shorter and its base is always nearer the girdle, while the left is longer and its base is farther removed giving to the organism a fundamental asymmetry. This disproportion of the antapicals is most apparent in the subgenus *Biceratium*, while in many species of the *C. macroceros* group the horns are approximately equal, the inequality appearing only on careful measurement. In a few cases in the *C. tripos* group the right horn is the longer one, as frequently in *C. schranki*, and sometimes in *C. arcuatum*.

These sustained proportions in the length of the two horns, and not infrequently in that of all the horns, are characteristic of the species and *they are preserved in autotomy*. An illustration of this appears in *C. gallicum* (figs. 13-15), *C. trichoceros* (figs. 16-19), and *C. biceps* (figs. 21-24), of normal individuals and others which have recently undergone autotomy. The orientation of the organism in flotation and in locomotion is obviously profoundly affected by its form and proportions. The preservation of the fundamental inequality of the antapical horns in autotomy is thus regulatory in character and may indeed be con-

trolled by factors analogous to, or the same as those that determine the original inequality of the antapicals at the time of schizogony. The nucleus is often found near the flagellar pore to the left of the center of the midbody and thus nearer to the base of the longer left horn than to that of the shorter right one. The radius of nuclear activity may be one of the factors influencing the inequality both in growth of the horns and in their subsequent autotomy and regeneration.

A striking instance of this regulatory phase of autotomy of the antapicals appears in those species of *Ceratium* such as *C. schranki* in which the proportionate lengths of the antapicals are reversed, that is the right horn is the longer and the left is normally the shorter one. *This reversal of proportions is usually retained in these species after autotomy.*

In *C. trichoceros* the two horns are nearly equal and vary considerably so that either horn may be the longer. In figures 16 to 19 are shown respectively a normal individual and several after autotomy, in all of which the proportions of the antapicals are approximately maintained. The apical is also shortened by autotomy but the proportion of the horn removed is less than that dropped from the antapicals, and the ratios which the stump bears to the antapicals are less regular than those between the two antapicals themselves. The following table gives the lengths of the three horns:

Ceratium trichoceros, length of horns in transdiameters.

	Apical from girdle	right	left
Fig. 16	8.4	14.	13.7
Fig. 17	3.	4.55	4.65
Fig. 18	5.8	2.6	2.7
Fig. 19	1.25	.65	1.

The location of the planes of autotomy is not a fixed one. Indeed, autotomy may be repeated in the same organism at levels successively nearer the base of the horns (figs. 20 and 24). It is found in different individuals at all levels from the very tip to the base of the horns. A series showing different levels at which autotomy occurs in *C. trichoceros* is found in figures 16 to 19, for *C. gallicum* in figures 13-15, and for *C. biceps* in figures 21-23. A much more complete series might be made for these or many

other species in which autotomy is prevalent. There is no universal or general tendency for autotomy to occur at any particular point. Autotomy in, or near the region of major flexure of the posterior horns is in some of my material more frequent than that in other regions, but there is no definite zone of autotomy here. This wide range in levels at which autotomy appears is in itself strongly indicative that the autotomy is not due to an internal localized structural weakness which renders the arms prone to break at given points, nor to mechanical strains of external origin resulting from impact and producing localized breakage of the arms as a result of the general form of the organism.

Autotomy does not always occur in both antapicals, or in all three horns, coincidently, nor does it always preserve the relative lengths of the horns characteristic of the species, but the proportion of instances in which these phases of the process are not evident is so small that they fall into the category of exceptions to a more general rule.

4. *Significance of autotomy.*—The wide-spread occurrence of this phenomenon is suggestive that it is a normal physiological process subject to regulation in common with growth and regeneration. It is obvious that the loss of the horns modifies the *specific gravity* of the organism only in the event of *unequal* distribution of density of the thecal wall. Evidence upon this point is only indirect. The horns are usually thinner-walled than the midbody, especially in their distal portions. Empty thecae sink to deeper waters as all catches from deeper levels show. The specific gravity of empty thecae may be greater than that of the whole organism. Autotomy leaves the thicker and presumably denser parts of the theca upon the organism and in so far tends to increase its specific gravity, thus tending to sink it to lower levels or assisting it in retaining its position at a certain distance *below* the surface when temperatures are lowered.

More patent still is the change in *specific surface* which must result from autotomy. This removes from the body the slender horns, those parts in which the number of units of surface to each unit of volume is greatest. By the process of autotomy the volume of the organism is reduced, but proportionately less than its surface. This results in a decrease in the specific surface and

therefore of the resistance which the molecular friction of the water affords to the sinking of the body.

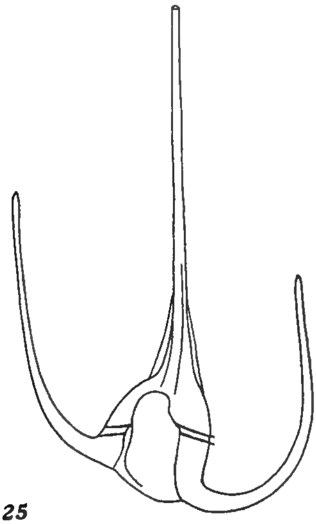
Ostwald (:03) has defined specific surface as the ratio of absolute surface to absolute volume. Computation of the actual surface and volume of a normal individual of *C. gallicum* and of the horns beyond a plane of autotomy midway in their length gives the following results, when S and V represent respectively the surface and volume before autotomy and s and v the corresponding measurements of the horns beyond the plane of section.

$$\frac{S}{V} > \frac{S-s}{V-v} \text{ or } 265 > 210.5.$$

The decline in specific surface is thus about 20.5%. Applying this to Ostwald's (:03) computations of the changes in molecular friction attendant upon changes in temperature we find that an increase of 20.5% in the molecular friction found in sea water at 20% would be equivalent to a drop in temperature of 7.43°. In other words, a normal *C. gallicum* before autotomy floating in water at 20°, would, other things being equal, be equally adapted to flotation in water at 12.57 by the autotomy of its horns midway in their length. Without autotomy its specific surface upon the lowering of the temperature would be in excess of its needs and would tend to maintain the organism in levels nearer the surface when once it entered them.

The cause of autotomy is not easily determined in view of the complex and largely unknown chemical and physical factors involved. Nevertheless the data of its occurrence are suggestive of the agency of certain of these factors, which may, moreover, be tested by experiment. *Ceratium* presents in its structure certain conditions peculiar among unicellular organisms, namely that of three distally projected protoplasmic horns which secrete upon their surface a continuation of the cellulose wall of the midbody. The synthetic processes of the cell go on only in the presence of the nucleus. The distance from the nucleus at which the metabolic processes involved in the secretion of cellulose can go on are possibly affected by temperature. Whether or not this results from the relation of temperature to the velocity of chemical reactions, we do not know. The facts are that in warmer waters the horns of practically all species are projected to a pro-

portionately greater distance from the nucleus than they are in colder waters. The contrast in length of horns of *Ceratium* from tropical and arctic waters has been a matter of frequent comment (see Chun '02) and the principle of the correlation of the processes of pelagic organisms with the function of flotation has often been noted [see Wesenberg-Lund (:00) and Ostwald (:03)]. Temperature thus bears a definite relation to the distance from the nucleus to which the horns of *Ceratium* may extend. In high temperatures this distance is greater than at low ones. So also



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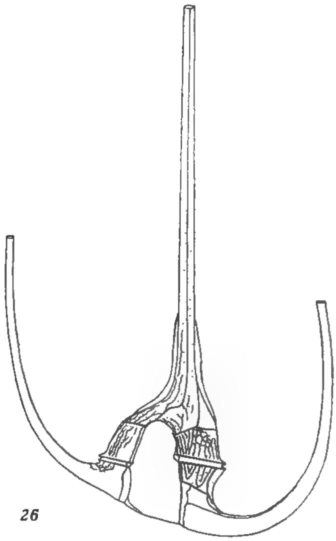

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Fig. 25.—Ventral view of a normal *Ceratium arcuatum*. × 155.
Fig. 26.—Ventral view of another individual after distal autotomy of the tips of the antapicals. × 160.

in the fully grown organism it may follow that the distance in the horn to which the normal processes of metabolism can be maintained is in a similar manner affected by temperature. A long-horned *Ceratium* entering a region of cooler water suffers, it may be, a reduction in the radius of action of nuclear activity and autotomy of a regulatory character follows. The suggestion naturally arises that under conditions of lowered temperature a ferment is produced or becomes effective which brings about a resolution of the wall and that the temperature regulates

the distance from the nucleus at which this reversal of the secretion process to one of resolution takes place. A suggestive parallel to this phenomenon is seen in the reversal of heliotropism of pelagic organisms by change in temperature described by Loeb ('93).

III. Regeneration in Ceratium.

1. *After schizogony.* In normal schizogony the naked portion of each segment is immediately covered by a duplication of that part of the ancestral thecal wall passed to its sister schizont.

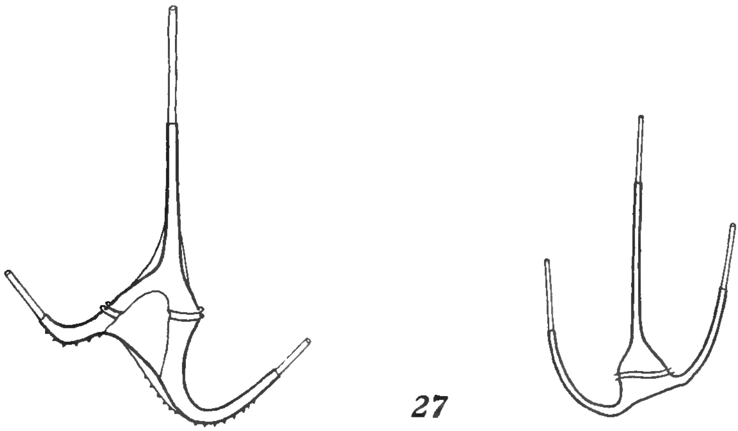

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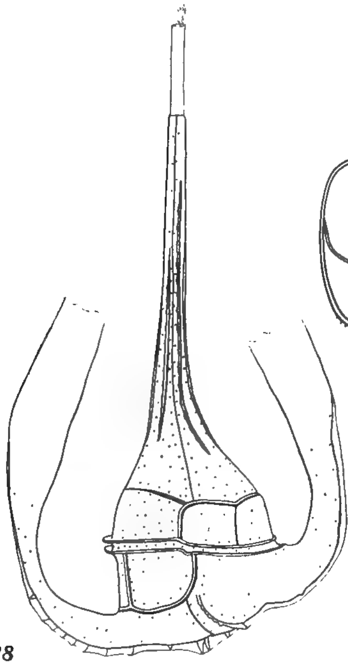
Fig. 27.—Ventral view of *Ceratium ostenfeldi* (?) and dorsal of *C. intermedium* showing proportional regeneration of all three horns presumably after autotomy. × 155.

When it first appears this newly formed wall is an exceedingly thin, structureless film which, by a process of thickening and superficial differentiation, rapidly takes on a facies similar to that of the inherited part of the theca. In all essential particulars this process is similar to the form regulation that attends the fission of other protozoa or of a planarian, but, owing to the considerable differentiation of the skeletal parts and the retention of half the ancestral skeleton, the resemblance to the process of regeneration of lost parts is the more striking.

2. *Regeneration after autotomy, or independently of it.* Autotomy is accompanied in this genus by the capacity for re-

generation of the horns. *Ceratium* exhibits, however, the capacity of increasing the length of its horns quite apart from autotomy. In species of the *C. macroceros* group in which the antapical horns have open tips the horns increase in length by simple extension of the protoplasm and its accompanying wall. In



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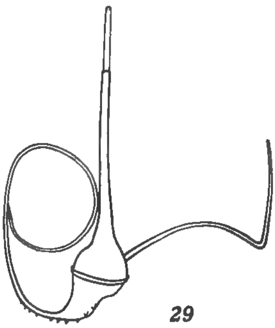

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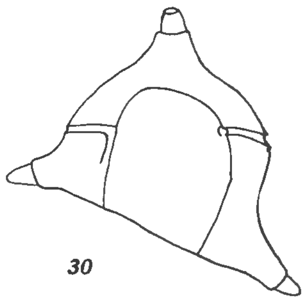

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Fig. 28.—Dorsal view of *Ceratium lamellicorne* (nomen novum = *C. tripos* forma *dilatata* Karsten = *C. dilatatum* (Karsten) Kofoid) showing renewed growth of the apical horns. × 440.

Fig. 29.—Dorso-lateral view of *Ceratium reticulatum spirale* showing the same. × 100.

Fig. 30.—Ventral view of *Ceratium divaricatum,* showing regeneration of all three horns after basal autotomy. × 100.

figure 27 are shown individuals of *C. intermedium* and *C. ostenfeldi* (?), in which all these horns are thus being extended apparently after autotomy, for, with this extension the total length is still within the norm of the species. The regenerated parts are exceedingly thin-walled and have apparently just formed and not

yet attained the length, thickness or surface markings characteristic of the species. This growth is apparently not a prolonged process, but one abruptly made, in like manner to the original growth of the horns. The evidence for this lies in the fact that the newly found portions of the wall are of approximately uniform texture throughout their length. They are also formed coincidently, since they are of similar texture on the three horns. Observations on many instances of regeneration in many species of *Ceratium* bear out the statement here made concerning their rapid and coincident formation. In figures 28 and 29 are shown similar instances of distal regeneration of the apical horn in *C. lamellicorne* and *C. reticulatum spirale.*

Regeneration proceeds in a slight measure, however, centrifugally from the stump of the horn. This is seen in the fact that occasionally individuals are found in which the protoplasm is naked distally or in which the distal part of the newly formed section of the horn is more delicate than the proximal. Such differences are, however, relatively insignificant and temporary.

3. *Regenerative growth independent of autotomy.*—In species having antapicals with closed tips such as those of the *C. tripos* and *C. furca* group I have found some evidence of distal extension of the antapical horns without preceding autotomy. In figure 26 is seen an individual of *C. arcuatum* which has undergone distal autotomy, and in figure 25 an instance of distal regeneration of the closed tips, apparently after autotomy. In the course of my examination of collections I have found numerous cases of subsequent distal regeneration of new tips after such distal autotomy in various species of the *C. tripos* group.

In a plankton collection taken July 12, 1904, in a haul from 75 fathoms to the surface there were a large number of *Ceratium divaricatum* in which there was renewed centrifugal growth at the *tips* of the closed antapicals and occasionally also of the tip of the apical as shown in figure 31. In some cases all three horns had renewed distal centrifugal growth, in others only the apical, and in still others either one or both of the antapicals. In no observed case, however, does the growth reach an extent which carries any of the horns beyond the normal range of variation in this species. This growth in *C. divaricatum* takes place at the

opposite end of the horn from that noted below in *C. californiense.* The prevalence of this renewed growth on the otherwise rugose thecae of the former species is strongly suggestive of a general readjustment of specific surface in this instance by prolongation of the horns brought about by growth of the regenerative type. In figure 30 is shown an instance of regeneration of all three horns *after autotomy* which left little of the organism save the midbody.

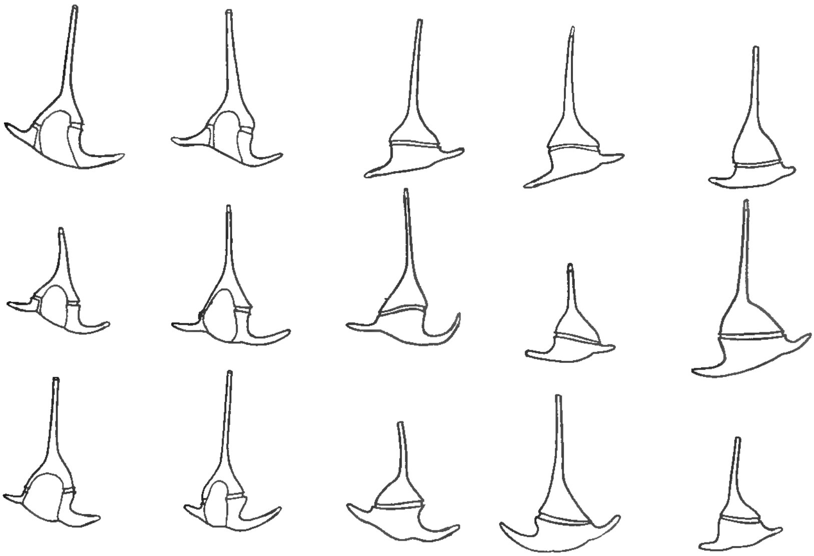

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Fig. 31.—Examples of regenerative growth in distal locations on the horns of *Ceratium divaricatum.* All from the same plankton collection. × 100.

In *C. californiense* (figs. 31 and 32) I have found one instance of *proximal growth in the antapicals without preceding autotomy.* In this species the tips are closed and the zones of new growth are at the *bases* of the antapical horns and the old thick-walled antapicals are carried out distally on the intercalated new zone. The apical horn on the other hand has a *distal zone* of new growth of a length corresponding to that which has taken place at the bases of the other two horns. It is obvious that this instance is not one of typical regeneration, for no parts

were lost prior to the renewed growth. The process and the function served are, however, in many aspects similar to those in typical regeneration.

4. *Regulatory nature of regeneration of the horns.*—In both of these types of regeneration or new formation of the horns, the extensions of the horns exhibit the same kind of form regulation as that which appears in normal growth. The proportions characteristic of the species are maintained by the coincident extension of both antapicals and of the apical also, in case it is proportionately short at the time of regeneration.

The regulatory character of the regeneration of the horns after autotomy and independently of it is evident on inspection of the table on p. 368. In nine of the fourteen cases of regeneration all three horns regenerate together. The apical does not exhibit this phenomenon in five instances and shows less growth than the antapicals in all but three cases. In three of the fourteen instances of regeneration the growth of the right horn exceeds that of the left, in three cases it equals it, while in the remaining eight it shows less growth. It appears that the same causes which control the extension of the horns in normal growth are operative in the majority of instances to control their extension in regeneration.

5. *Significance of regeneration.*—It is obvious that increase in the length of the horns, of those parts of the body in which the number of units of surface per unit of volume, is greatest, results in a relative increase of surface and a rise in the specific surface of the organism. Increased specific surface is an adaptation of flotation in water of higher temperature. Individuals in which these extensions have occurred will be able to maintain their customary location in the face of a rise in temperature up to a certain point, or to retain their position at given levels in warmer waters into which they might move. The extent to which these distal growths of the horns may be operative in adjustments of capacity for flotation may be illustrated in the case of *C. californiense.*

This specimen with renewed growth (figs. 32 and 33) was taken May 28, 1904, 10 miles west of Pt. Loma over Cabral's Banks in a haul from 75 fathoms. Surface waters on that day

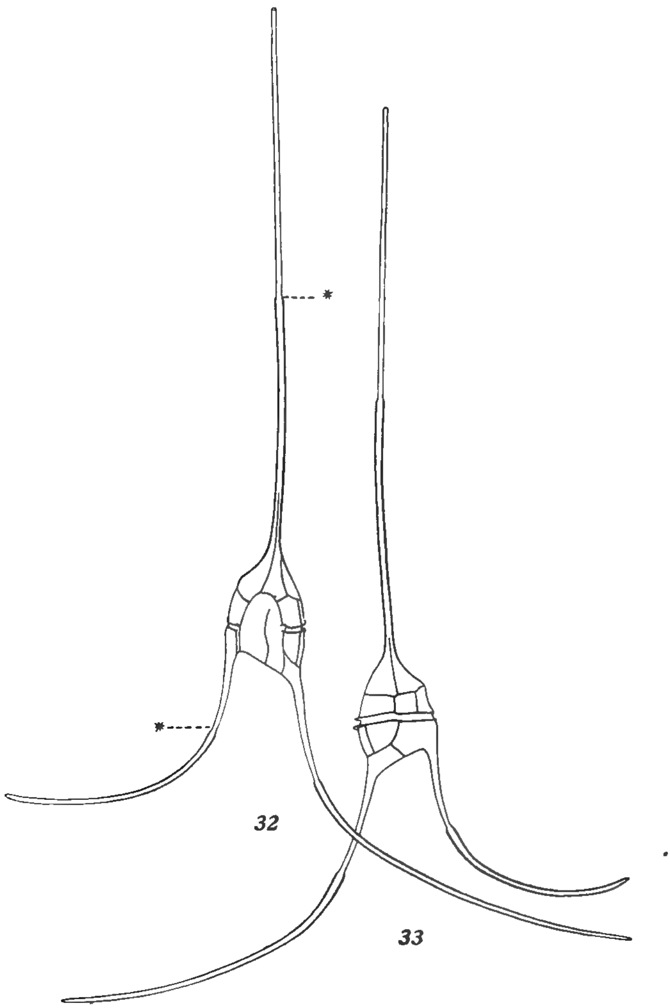

Fig. 32.—Ventral view of *Ceratium californiense* showing regenerative growth at the distal end of the apical and proximal ends of the antapical horns. Points of junction of new and old growth marked by an asterisk. × 300.

Fig. 33.—Dorsal view of the same. × 300.

off Coronado Pier had a temperature of 20.8°. Temperature of water off San Diego pumped from a depth of 70 fathoms on June 30, 1903, was 14.2°, on July 1 was 14.7°, on July 2 from 72 fathoms, was 15°, on July 3 from 70 fathoms, was 14.7°, on July 7 from 72 fathoms was 15°, and on July 9 from 72 fathoms was 15.5°. It is possible that the extreme limits from which this particular specimen might have been taken lie approximately between about 14° and 20.8°. If it had taken on its new growth to adjust its flotation in water which had risen to 20.8°, the 19% increase in specific surface would, according to Ostwald's (:03, p. 62) table of temperatures and molecular friction, accommodate the organism to an advance from 12.25° to 20.8°, or to a rise of 8.55° Tests of vertical distribution of temperature made off San Clemente Island in July, 1905, with the self-closing water bottle (see Kofoid :05) indicate that a decline of temperature to this extent occurs within approximately 200 fathoms of the surface. This distance, 200 fathoms to the surface, is quite within the range of the possible distribution of this organism. This is a somewhat close approximation between the increase in specific surface caused by the renewed growth and the changes in molecular friction due to the range of temperatures in the possible habitat of the species. This close agreement between Ostwald's experimental determinations and my computations of the changes in specific surface of this pelagic organisms are all the more striking and significant if the probability of error in the determination of the specific surface of so small and irregular a body as that of *C. californiense* is borne in mind and also the certainty that other factors enter to modify the process of adjustment, such as alterations in specific gravity which might follow from changed proportions of thin and thick thecal wall, and from modifications in metabolism and in cell contents attendant upon increased illumination and reduced pressure.

Summary.

In some Dinoflagellata ecdysis, or the shedding of the total exoskeleton does not occur.

In those genera, such as *Ceratium,* in which the theca is shared between the daughter schizonts at schizogony, compensatory re-

generation of the newly forming part of the exoskeleton occurs. Skeletons of senile facies may be removed by exuviation, plate by plate, often at the time of schizogony. This exuviation makes possible readjustments of specific gravity and specific surface to changing conditions of flotation.

Autotomy of the two antapicals, or of all three horns is of widespread occurrence among many species of Ceratium. It is more abundant in collections from deeper levels than in those from the surface. It is caused by local resolution of the cellulose wall and is regulatory in character, preserving in the horns after autotomy the proportions characteristic of the species. Autotomy assists in the adjustment of specific surface and possibly also of specific gravity to changing conditions of flotation, especially as affected by temperature.

Regeneration of the horns with or without preceding autotomy may occur in all three horns. It is also regulatory in character and tends to preserve the norm of the species.

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CONTRIBUTIONS FROM THE LABORATORY
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MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO.

XXII.

NOTES ON SOME OBSCURE SPECIES OF *CERATIUM*.

BY
CHARLES ATWOOD KOFOID.

The publication of the preceding paper (Kofoid ('08)) has necessitated the recognition of certain species in the genus *Ceratium* which either have not appeared in the current literature dealing with this polymorphic genus, or if they have been cited, the nomenclature used requires revision.

In 1874 Ehrenberg, in a paper published in the centennial volume of the "Gesellschaft für Naturforschenden Freunden zu Berlin" under the title "Die das Funkeln und Aufblitzen des Mittelmeeres bewirkenden unsichtbar kleinen Lebensformen" figured and described briefly several species of *Ceratium* which seem to have been overlooked generally by subsequent investigators. Ehrenberg's paper has escaped the notice of later monographers, even of Bütschli ('83-'87) and of Schütt ('95 and '96), for neither lists it in his bibliography of the *Dinoflagellata*.

Among other organisms of the plankton this paper describes four species of *Ceratium* as of the genus *Peridinium*, to wit: *P. Trichoceros, P. Candelabrum, P. eugrammum*, and *P. Seta*. Of these *P. candelabrum* was later recognized by Stein ('83), who, however, reduced *P trichoceros* to a synonym of *C. tripos*,

and *P. Seta*, to a synonym of *C. fusus*, in the explanation of his Tafel 16, while *P. eugrammum* is referred to *C. furca*, in the explanation of his Tafel 15.

It is not improbable that the reduction of these species of Ehrenberg's to synonyms by Stein ('83) is due to Stein's knowledge only of an earlier paper of Ehrenberg's ('60) in which he briefly diagnosed these species, but without figures, in the absence of which their recognition is difficult, if not impossible. Later authors have, with the exception of Saville-Kent ('81-'82), concurred in Stein's opinion.

I have elsewhere (:07) noted the correctness of Ehrenberg's recognition of *C. eugrammum*. I wish here to revive two of his other species of *Ceratium*, which are equally valid, and to note the instances in which several of them have crept into literature under new names in recent years.

Ceratium trichoceros (Ehrbg.).

Ehrenberg ('60), p. 791, as *Peridinium Trichoceros.*
Ehrenberg ('74), p. 3, Taf. (1), fig. 1, as *Peridinium Trichoceros.*
Saville-Kent ('80-'81), vol. 1, p. 457, as *Ceratium seta.*
Stein ('83), explanation of Taf. 16, as a synonym of *C. tripos.*
Karsten (:06), Taf. 22, fig. 31b, as *C. flagelliferum* Cleve; fig. 32a and b, as *C. flagelliferum* forma *crassa* n. var. The latter figure is questionably referred to *C. trichoceros* by me.
Kofoid (:08), p. 362, figs. 15-19.

This species of Ehrenberg's is well defined by its rigid habit of growth, the wide-spreading major flexures of the antapicals, and the slender horns with pointed closed tips. Its three horns are subparallel and the antapicals are usually noticeably serrate along their posterior margin toward their major flexures.

It has probably been confused in the past with *C. flagelliferum* Cleve (:00), a form of *C. inflexum* Gourret ('83), which has more flexible or variously incurved or recurved antapicals and exhibits in general a more lax habit of growth than *C. trichoceros.* The tips of the antapicals of *C. inflexum* are contracted, usually have a small terminal pore and are sometimes swollen, differing in these particulars from the pointed closed tips of *C. trichoceros.* *C. inflexum* also lacks, as a rule, the prominent posterior serrations of *C. trichoceros.*

Ceratium seta (Ehrbg.).

Ehrenberg ('60), p. 792, as *Peridinium Seta.*
Ehrenberg ('74), p. 3, Taf. (1), fig. 1, as *Peridinium Seta.*
Saville-Kent ('80-'81), p. 457, as *Ceratium seta.*
Stein ('83), explanation of Taf. 15, as a synonym of *C. fusus.*

A careful examination of the species of the *Ceratium fusus* group which I have recently made at San Diego convinces me that Ehrenberg was correct in distinguishing *C. seta* as a species distinct from *C. fusus.*

Ceratium seta has a less broadly fusiform midbody, its trans-diameter averaging 10 μ less than that of *C. fusus.* Its surface is less rugose, its curvature usually more pronounced, and its right antapical uniformly suppressed, whereas this horn is short but uniformly present in *C. fusus.* Another striking difference lies in the fact that the hypotheca exceeds the epitheca in the former species, but these relations are reversed in *C. fusus.*

Gourret ('83) describes, as *C. fusus* var. *extensum* and *C. longirostrum*, certain long-horned forms resembling *C. seta.* A statistical study of material from the oceanic plankton off San Diego leads me to regard these as forms of one species, *C. extensum* (Gourret), which, however, is distinct from *C. seta.*

Ceratium biceps Clap. et Lachm.

Claparède et Lachmann ('58-'59), pp. 400-401, pl. 19, fig. 8.
Gourret ('83), pp. 55-56, pl. 1, fig. 19, as *C. Berghii.* Symmetry reversed in figure.
Okamura and Nishikawa (:04), p. 128, pl. 6, fig. 25, as *C. fusus* var. *stricta* nov. var. prov.
Kofoid (:07), p. 133, as *C. strictum.*
Kofoid ('08), p. 00, figs. 21-24, as *C. biceps.*

In my opinion Claparède and Lachmann described as *C. biceps* an individual which had recently undergone autotomy and had in consequence relatively short apical and left antapical horns. Their figure will bear the closest comparison with such mutilated specimens. Later Gourret ('83) gives a reversed figure which may be referred provisionally to this species. Okamura and Nishikawa (:04) were the first to publish a typical figure showing the normally developed horns, but they did not recognize the similarity of the species with which they were dealing to that

previously described by Claparède and Lachmann, or Gourret; nor did they call attention to the short forms of this species which result from autotomy. When this phenomenon of autotomy is borne in mind we may utilize Claparède's and Lachmann's description and revive their name for this well defined species.

Ceratium biceps is a large species differing from *C. fusus*, and *C. seta* in its greater length, and from *C. extensum* in the presence, uniformly, of a right antapical horn or its truncated stump, in its larger midbody and in the less curved, slightly deflected, left antapical horn.

Ceratium lamellicorne nom. nov.

Karsten (:05), p. 132, Taf. 19, figs. 9, 10, as *C. tripos* forma *dilatata*.
Kofoid (:07), p. 171, pl. 4, fig. 25, as *C. dilatata* (Karsten).
Karsten (:07a), Taf. 48 (14), figs. 10a, 10b, as *C. tripos platycorne* Daday. Karsten's Taf. 51, figs. 4a, 4b, also called by him *C. tripos platycorne* Daday, is the typical *C. platycorne*.
Kofoid (:08), p. 185, fig. 28, as *C. lamellicorne*.

This is a small species of the *C. platycorne* group, with the antapicals expanded into a thin sheet in the plane of the three horns. It differs from the true *C. platycorne* in its smaller size and relatively shorter antapicals which are also narrower with a more regular curvature and a more uniform width throughout their length. They lack the characteristic swelling found on the median margin of the antapicals of *C. platycorne*. Karsten's earlier figures (:05), designated by him as *C. tripos* forma *dilatata*, are in my opinion *C. lamellicorne*. His later figures (:07) are in part (Taf. 48, figs. 10a, 10b), of the *C. lamellicorne* type and in part (Taf. 51, figs. 4a, 4b) of the type originally described by Daday ('88) as *C. platycornis*. On the grounds above stated I regard the two species as distinct.

In his earlier paper Karsten (:05) makes no mention of the species described by Daday and we are left without any evidence in his brief descriptive text as to whether or not he regarded the two forms as distinct. In his later paper (:07, p. 406) he discusses the question and concludes that his forma *dilatata* is only a young form of *C. platycorne*, in which the antapicals have not

as yet expanded to the size that they later attain in the older stage.

As above stated, *C. lamellicorne* is smaller than *C. platycorne.* This applies to the length of the horns, which, as I have shown in the preceding paper, might be expected to undergo changes in length during the life of the individual by processes of autotomy, regeneration, or growth of regenerative type. Lateral expansion of the median margin of the antapical horns is also theoretically possible. The midbody, however, is typically larger in *C. platycorne* than in *C. lamellicorne.* I have no evidence that the midbody of *Ceratium* is subject to an increase in size comparable with that which may occur in the horns.

A consideration of the conditions pertaining to the skeleton during schizogony, especially the fact of compensatory regeneration of the new skeletal moiety, and the essential uniformity of individuals in chain, would seem to preclude the existence of any such young and old stages of the individual with accompanying differences in dimensions due to growth, such as would necessarily follow from Karsten's point of view with regard to these two forms. I find no such prevalence of intergrades as the idea that *C. platycorne* is the old stage of *C. lamellicorne* would lead us to expect. An examination of a large number of sketches of these two species of *Ceratium* from the oceanic plankton off San Diego leads me to believe them to be distinct species with a constant size difference and not age forms of one.

Karsten's (:05) name *dilatata* is preoccupied by Gourret's ('83) *C. dilatatum.* Gourret seems also not to have known of Ehrenberg's ('74) description of *C. candelabrum* and among other names which he has applied to various forms of that polymorphic species, he uses *C. dilatatum.* Because of Gourret's prior use of this name I here propose for this smaller species the new name of *C. lamellicorne.*

Zoological Laboratory, University of California,
April 2, 1908.

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(Sonderabdruck aus dem »Zoologischen Anzeiger« Bd. XXXII. Nr. 7
vom 1. Oktober 1907.)

The plates of Ceratium with a note on the unity of the genus.

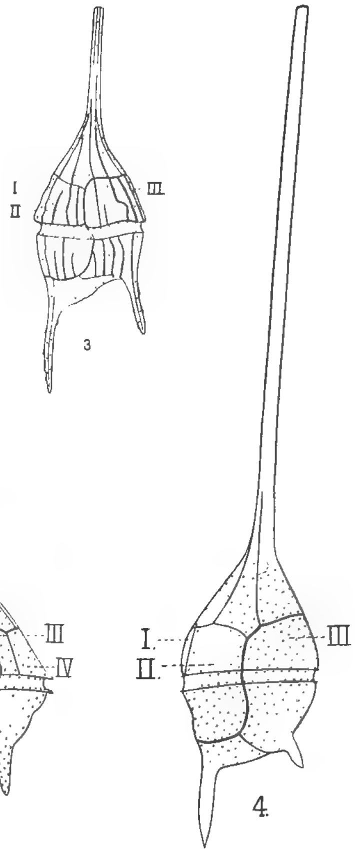
By Prof. Charles Atwood Kofoid.
(Zoological Laboratory, University of California, Berkeley.)

(With 8 figures.)

In the course of the preparation of an account of this genus as i occurs in the plankton of the Pacific off San Diego I have had occasio: to determine the plates of the theca and find my results at varianc with those hitherto reported. This has led me to verify, in most parti culars, my conclusions here presented, on a large number of individual representing at least sixteen species of *Ceratium* including representa tives of the genera *Ceratium* sensu stricta, *Amphiceratium*, *Biceratiu* and *Poroceratium* of Vanhoeffen (1896) and has therefore enabled m to reach conclusions regarding the validity of this proposed dismember ment of the genus *Ceratium*.

of Bergh (1881)[4], Hensen (1885)[5], Entz (1902)[6] and Zacharias (1906)[7], along with typical *C. furca* and *C. lineatum* (the so-called *C. furca* var. *baltica* Moeb. nomen nudum), but in no case has it been accorded specific recognition, except by Vanhoeffen (1897)[8] who described it as *Biceratium debile*.

In the course of my investigations in the Dinoflagellata[9] of the plankton



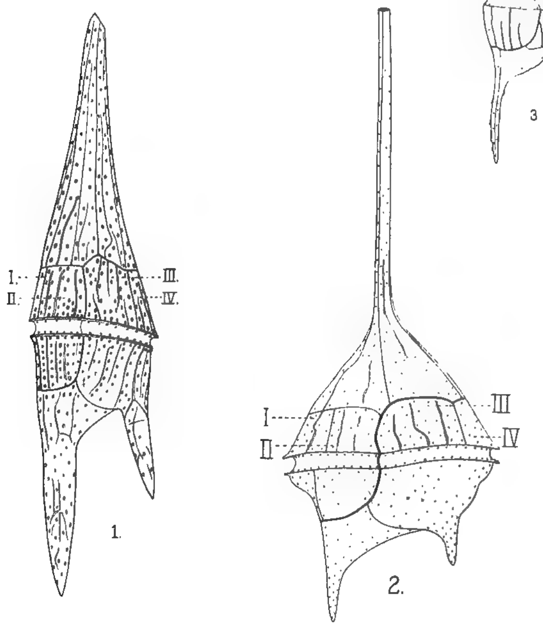


Fig. 1—4. Dorsal views of thecae of *Ceratium furca*, *C. lineatum*, *C. eugrammum* and *C. teres*. I—IV, precingular plates. $\times$ 500. Original.

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of the Pacific from Alaska to San Diego I have found this species in a large number of collections and am convinced of its distinctness from both *C. lineatum* and *C. furca*, with neither of which it intergrades, and that it is, in all probability, the form the Ehrenberg recognized and must therefore be designated as *C. eugrammum* (Ehrbg.).

The accompanying figures give, for comparison, dorsal views of four species, three of which have been subject to great confusion in the faunistic literature of the group and the fourth (*C. teres*) has been rerently described by me.

C. eugrammum is the smallest species in the genus. It has a relatively narrow midboy with steep lateral margins of the epitheca. Its antapicals are straight, and usually not diverging, and the hypotheca is but little contracted between the girdle and the bases of the antapicals. It differs from *C. furca* in its smaller size, greater delimitation of apical

Species	Relation of apical horn to epitheca	Divergence of margins of epitheca from perpendicular to plane ofgirdle	Postobliquity	Transdiameter	Ratio to transdiameter of axial altitude of midbody.
C. furca	gradually merged	right 14° (10°—18°) left 16° (11°—19°)	42° (35°—60°)	35 (30—50) μ	1:2,25 1,5—3,
C. lineatum	delimited	right 30° (24°—37°) left 38° (33°—42°)	18° (15°—21°)	58 (50—67) μ	1:1,1 (1—1,25)
C. eugrammum	delimited	right 23° (15°—27°) left 26° (25°—31°)	24° (22°—27°)	25 (19—30) μ	1:1,4 (1,3—1,5)
C. teres	delimited	right 20° left 30°	12° (6°—19°)	37 (30—40) μ	1:1.5 1,3- 1,8)

horn from midbody, shorter antapicals, marked linear striae and more delicate habit. From *C. teres* it differs in the more robust habit and presence of striae, in the straight, rather than convex, sides of epitheca and hypotheca and in the absence of distal contraction of the latter. It thus lacks entirely the broadly fusiform outline which *C. teres* presents. From *C. lineatum* it differs in its narrower midbody and steeper slopes of the antero-lateral margins of the epitheca. It is evident that *C. lineatum* and *C. eugrammum* are closely related as shown by their form and surface markings. They differ however in one important structural character, viz: — the precingular plate (fig. 2 *IV*) which is present in *C. lineatum* but apparently not in *C. eugrammum*. The normal number of precingular plates in the genus *Ceratium* is three but in *C. lineatum* and *C. furca* in some individuals, at least, an additional suture line passes from the suture between the apical and precingular series to the girdle plate, spliting the right precingular into two parts. This accessory

suture line is optically similar to sutures other than that of the line of cell-division which is more heavily marked.

The appended table of diagnostic characters based on measurments of a number of individuals will serve more clearly to define the characters of the species in question. Northern forms (Alaskan) are absolutely larger in dimensions of the midbody than southern (San Diego), but horns, especially the apical, tend to be relatively longer in the individuals from warmer waters.

Both *C. lineatum* and *C. furca* are common cosmopolitan species alike in neritic and oceanic plankton. *C. eugrammum* is likewise cosmopolitan and *C. teres* bids fair to exhibit a similar range as it is widespread in Pacific waters. These two species are, however, both relatively rare, perhaps in part because of the fact that their small size permits them to slip through the mesh of the silk gauze used in plankton nets.

A few filter catches which I have examined have not indicated any abundance of these two species equal to that of *C. furca* and *C. lineatum.* They are apparently not well established dominant species and perhaps belong in the category of less sturdy mutants from some member of the *C. furca* group.

Berkeley, California, March 23, 1907.

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In agreement with Stein (1883), Bütschli (1883—1887) and Schütt (1895) as opposed to Klebs (1884) I regard the plates of the Dinoflagellates as structurally stable features, subject, of course, to variation and abnormalities, and even to irregularity in a few species, but of sufficient constancy to afford a most satisfactory basis for classification, a basis, moreover, now widely adopted as a criterion for generic distinction among the Dinoflagellata.

As Schütt (1895) has so well shown, the superficial lists, even the primary ones, are in no way a safe criterion for the analysis of the thecal structure. This can be accurately determined only by following the sutures. These, however, are obscure, and are often only dimly suggested by vaguely outlined overlapping margins of the plates that appear best upon deep focus on the thecal wall. Prolonged treatment in warm alkalis does not always bring about separation of the plates along the suture lines though it is of great assistance in resolving the structure.

Actual separation of the plates in situ is the only safe guide to an analysis of the thecal wall, but a failure to cause separation under treatment does not afford a valid basis to deny the existence of a suture, since it may be merely the result of the condition in which the material is found at the time of examination. I am inclined to believe, as a result of many tests, that all reports of three apical plates in *Ceratium* rest upon material imperfectly separated, and that the variation in the splitting of the apical and left antapical horn reported by Klebs (1884) is more a matter of imperfect separation than of a morphological variation in suture lines and number of plates. In other words I have found *Ceratium* far more constant in the matter of sutures and plates than it has been reported to be.

Stein (1883) characterized the genus and distinguished it from *Peridinium*, with which Ehrenberg (1835) had confused it, and from which Claparède and Lachmann (1858—1859) had subsequently separated it on the basis of the horns, by its plates, which he defined as composed »aus 3 Basalien und 3 Frontalien am Vorderleibe, und aus 3 Basalien und einer Endplatte am Hinterleibe«. Bütschli (1883—1887), probably influenced by Klebs' [illegible] ds the theca as composed anteriorly of three [illegible] times more) apical plates, and [illegible] cal plate. Schütt (1896) regards [illegible] e intermediate plates and four end plates and the »Unterschale« as made up of three equatorial plates and one end plate. He notes also the presence of several girdle plates.

Entz (1905) was the first investigator to establish the existence of

four apicals. In the case of *C. hirundinella* and *C. candelabrum* he finds four plates in each of the series which he designates as pre-and post-equatorials. He finds but one antapical plate, and adds much to our knowledge of the obscure details of the ventral plate, longitudinal furrow and attachment region.

I shall use the term apical for the anterior series of plates only, and shall designate the series anterior to and contiguous to the girdle as precingular (prec.), and that posterior to and contiguous to it as postcingular (postc.), and the posterior ones as antapicals (antap.). These names are distinctive of the four series and are widely applicable throughout the Dinoflagellates.

The theca of *Ceratium* is composed of four series of plates, two

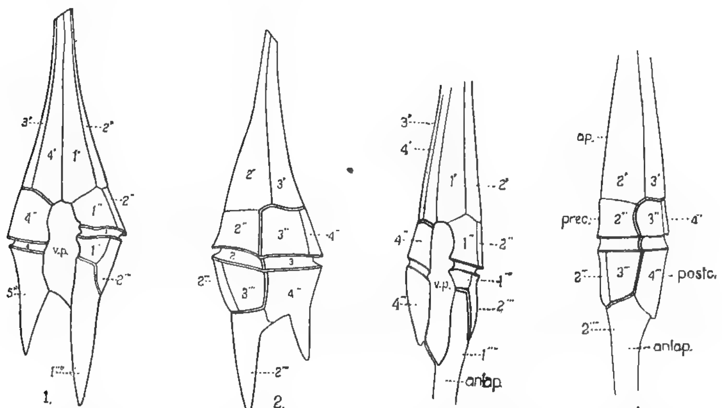


Fig. 1. Ventral view of *Ceratium furca.* × 350. In this and the following figures the apical plates are numbered 1′—4′, the precingulars 1″—5″, the postcingulars 1‴—4‴, the antapicals 1⁗ and 2⁗, and the girdle plates (numbered only in Fig. 1 and 2) 1—4.

Fig. 2. Dorsal view of *C. furca.* × 350.

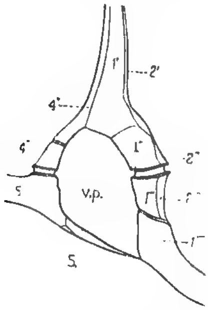
Fig. 3. Ventral view of *C. fusus*, region of the midbody only. × 530. *ap*, apical series; *prec*, precingular series; *postc*, postcingular series; *antap*, antapical series of plates; *v.p*, ventral plate.

Fig. 4. Dorsal view of *C. fusus.* × 530.

in the epitheca anterior to the girdle, and two posterior to it in the hypotheca, with a series of four narrow trough-like girdle plates between. There is in addition to these the so-called ventral plate (v. p.) which is a thin membranous sheet scarcely comparable with the rest of the thecal wall in structure and not belonging to any of the series, but intercalated on the ventral face in the midventral line extending through both the pre- and postcingular series.

There are always, in all species I have thus far examined on this

point, four apical plates (Fig. 4 *ap* 1′—4′). Plates 1′ and 4′ lie on the ventral surface separated from each other by a midventral suture which rises from near the apex of the ventral plate (Fig. 5). This suture is not always easily seen, more readily, perhaps, in the *C. fusus* group (Fig. 4) than in those of the *C. furca* (Fig. 1) group. It is also less readily separable on treatment with reagents. This probable accounts for the fact that in Stein's (1883) figures of *C. furca* this suture is omitted, while it is given by him for *C. fusus.* The fact that these two plates frequently adhere to each other after the other sutures of the apical series separate has given rise to the earlier statements that *Ceratium* has but three apical plates. These two plates are somewhat more slender than the two on the dorsal side. The sutures which separate the ventral and dorsal pairs lie on the ventro-lateral faces and are consequently less easily followed in many species. These rest posteriorly upon the precingular series of four plates, instead of three as usually reported



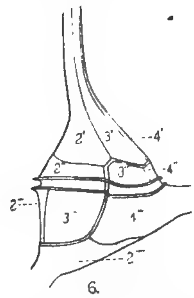


Fig. 5. Ventral view of *C. intermedium*, region of the midbody only. × 350.
Fig. 6. Dorsal view of *C. intermedium.* × 350.

(Fig. 4 *prec* 1″—4″). The line of fission, marked in all the figures by two parallel lines divides these into a right and left pair on the middorsal line. Precingular plates 3″ and 4″ of my nomenclature seem to have been regarded as a single plate by other investigators, except by Entz (1905), by the omission of the suture separating them or failure to note its significance when detected.

The postcingular series (Fig. 4 *postc* 1‴—5‴) is composed of 5 plates, of which two (1‴ and 5‴) are small and lie on the ventral face of the hypotheca. Plate 1‴ is always small and covers a relatively small area posterior to and to the left of the flagellar pore, and generally has a somewhat oblique posterior border. Plate 5‴ forms the ventral face of the right antapical. Its presence is obscured by the fact that the suture which separates it from plate 4‴ lies in the frontal plane passing from the girdle posteriorly along the lateral margin of the hypotheca to

the tip of the right antapical, and thence along its inner (left) margin to the base of the right horn at the upper angle of the oblique postmargin. It is thus in contact dorsally with plate 4‴. Its left median margin is in contact with the ventral plate (*v.p*) and immediately behind the ventral plate it is in contact for a short distance (Fig. 5) with the right tip of the mesad projection of the dorsal antapical (2⁗).

The other plates of the postcingular series, 2‴—4‴, lie on the dorsal side of the epitheca. Plate 2‴ is usually a narrow plate on the left margin of the hypotheca; 3‴ lies to the left of the fission line. Plate 4‴ lies to the right of this line and extends posteriorly to the tip of the right antapical horn, forming its dorsal side only. The right horn thus belongs entirely to the postcingular series of plates.

The left on the other hand is made up of a pair of posterior or antapical plates (1⁗ and 2⁗), one of which (1⁗) is ventral and the other (2⁗) dorsal. The suture line separating these two plates lies in the mid-frontal plane and is frequently marked by a primary list, but is never easily followed as a suture in situ because of its position. The ventral antapical plate (1⁗) is extended anteriorly on the ventral face of the hypotheca till it abuts against postcingulars 1‴ and 2‴ and its mesad margin borders the ventral plate. The dorsal antapical forms not only the dorsal side of the left antapical horn but covers the dorsal face of the posterior part of the hypotheca, meeting postcingular plates 2‴, 3‴ and 4‴. A long narrow shank (Figs. 5 and 6) projects to the right, especially in species of the *C. tripos* group, forming the oblique postmargin between the bases of the antapical horns and meets at its squarish tip the posterior angle of postcingular 5‴ of the right antapical horn. The antapical plates are bounded anteriorly by the fission line to the point of the suture between plates 3‴ and 4‴.

The girdle is composed of four narrow trough-like plates (Figs. 1, 2, 1—4) which part most readily at the fission line in the middorsal suture, and less readily in lateral sutures near those which separate precingulars 1″ and 2″ and 3″ and 4″. This suture and the fact that the left antapical horn is composed of two plates, in so far as I can determine, has not been previously noted. It is one of the sutures most difficult to demonstrate.

The distinction in size between the long left antapical horn and the short right one holds throughout practically all the protean species of this genus. It is least apparent in the long-horned species of the *C. tripos* and *C. macroceros* groups and most pronounced in the *C. fusus* group. This distinction in size is emphasized by the fact that the obliquity of the postmargin brings the base of the right horn anterior to that of the left, and by the fact that its base comes nearer to the girdle

on the lateral margin of the midbody especially in species of the *C. tripos* group (Fig. 5).

This difference in the horns rests upon the fundamental distinction in their morphological relations. The right horn belongs to the postcingular series of plates, and the left to one posterior to this. This constancy in the relations of these horns thus rests upon the constant generic character of the number and relations of the thecal plates.

As shown in the accompanying figures, the several genera proposed by Vanhoeffen (1896) all have the same thecal structure in the matter of the number and relations of the plates in the several series. The differences lie only in the form and proportion of the plates which vary their relations mainly in the extent of their contiguity. *C. fusus* (Fig. 3—4)

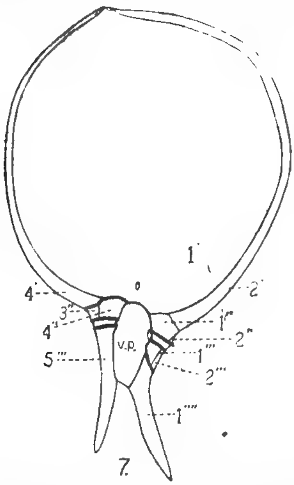


Fig. 7. Ventral view of *C. gravidum*. × 150.

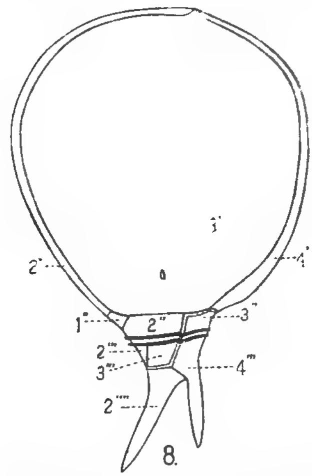


Fig. 8. Dorsal view of *C. gravidum*. × 150.

represents Vanhoeffen's genus *Amphiceratium*, *C. furca* (Figs. 1, 2) his *Biceratium*, *C. gravidum* (Figs. 7, 8) his genus *Poroceratium*, and *C. intermedium* (Figs. 5, 6) his genus *Ceratium* sensu stricta, for which he selected as a representative species, *C. labradoricum* Schütt (= *C. arcticum* Clap. et Lachm.). This is well represented by my figures of the closely related *C. intermedium*.

The fact that the plates of these proposed genera are all identical is in my opinion an imperative reason for rejecting the proposed dismemberment of the genus *Ceratium*. Since the pore which perforates the epitheca of *C. gravidum* is absent in the very closely related *C. praelongum* and is subject to great variation in the degree of its development in *C. gravidum*, even to its suppression, I regard this structure as not affording a basis for the generic distinction of the genus *Poroceratium*.

The mere modifications in the form and proportions of plates, even though they result in the development or suppression of antapical horns, is not, in my opinion, an adequate ground for generic distinctions among the Dinoflagellates. If applied to *Ceratium hirundinella*, for example, it would become necessary to erect new genera for the three, four and five horned varieties or growth forms of this variable species! The unity of the genus *Ceratium* rests upon the well-defined character of the number of its plates and their relations.

Berkeley, June 7, 1907.

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On Ceratium eugrammum and its related species.

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(With 4 figures.)

In 1859 Ehrenberg[1] described a small species of *Ceratium*, related to *C. lineatum*, as *Peridinium eugrammum* but did not figure it until 1873[2] in a paper whose title failed to suggest its contents. This paper is not cited in any of the earlier or more recent bibliographies of the Dinoflagellata except indirectly in Bütschlis Tierreich monograph. Stein (1883)[3] cites this species in his monograph as a synonym of *C. furca*, a view acquiesced in there after by all other investigators. This species of Ehrenberg has reappeared in subsequent literature in the figures

[1] Ehrenberg, C. G., Über das Leuchten und über neue mikroskopische Leuchtthiere des Mittelmeeres. Monatsber. k. preuß. Akad. Wissensch. Berlin 1859. S. 727—738, 791—793.

[2] Ehrenberg, C. G., Die das Funkeln und Aufblitzen des Mittelmeeres bewirkenden unsichtbar kleinen Lebensformen. Festschrift zur Feier d. 100jährigen Bestehens d. Ges. naturforsch. Freunde in Berlin 1873. p. 1—4, 1 Taf.

[3] Stein, F., Der Organismus der Infusionstiere. III. Abt. 2. Hälfte. Die Naturgeschichte der Arthrodelen Flagellaten. 30 S. 25 Taf. 1883.